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Woody plant distributions along an Amazon-to-Andes elevation gradient

Evolutionary trends and tendencies

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“One steps through the wall of the tropic forest, as Alice stepped through the looking glass; a few steps, and the wall closes behind. The first impression is of the dark, soft atmosphere, an atmosphere which might be described as ‘hanging,’ for in the great tangle of leaves and fronds and boles it is difficult to perceive any one plant as a unit; there are only these hanging shapes draped by lianas in the heavy air, as if they had lost contact with the earth (...) the tree boles erupt out of heaped masses of decay, as if the ground might be almost any distance beneath. The trees are so tumultuous and strange that one sees them as a totality, a cumulative effect, scarcely noticing details.”

Peter Matthiessen, The Cloud Forest:
A Chronicle of the South American Wilderness

“The more one learns of this intricate interplay of soil, altitude, weather, and the living tissues of plant and insect (...), the more the mystery deepens. Knowledge does not dispel mystery.”

Nan Shepherd, The Living Mountain:
A Celebration of the Cairngorm Mountains of Scotland

Abstract

With high taxonomic turnover and exceptional levels of endemism, tropical montane forests are one of the most biodiverse ecosystems on the planet. The taxa within these forests frequently occupy narrow elevational ranges, and display upslope migration rates insufficient to track predicted temperature increases. Consequently, tropical montane forests and the diversity within them are expected to be susceptible to declines in abundance and potential extinction under ongoing environmental change. Substantial changes to biodiversity patterns across elevation may have significant consequences for the carbon and nutrient cycles as well as the regulation of hydrological processes provided by these forests.

In this thesis I examine the diversity and distribution trends of woody plants across a tropical montane forest elevation gradient on the Amazonian flank of the Peruvian Andes, stretching from 425 to 3625 m asl. I consider the influence of the major environmental changes which occur over elevation, such as decreasing temperature. A particular focus is on the transitions which occur at the cloud-base ecotone, above which forests are defined by frequent and prolonged cloud immersion. I apply an evolutionary perspective, using phylogenetic approaches throughout this research. Closely related evolutionary lineages are frequently similar in terms of their ecology and functional characteristics, yet the influence of this tendency on the elevational distribution pattern of woody plants within tropical montane forest has received limited attention

Using census data from a network of one-hectare plots, in combination with phylogenetic information, covering a breadth of vascular plant diversity, from angiosperms and gymnosperms to pteridophyte tree ferns, I investigate the influence of evolutionary heritage on elevational distribution trends at the genus level. I further employ these plot data to reflect on the differences between taxonomic and phylogenetic richness patterns across elevation. A deeper consideration of the way variation in the evolutionary age structure of communities can influence diversity trends is also undertaken. In order to test the consistency of elevational patterns between genus and species scales,

I conducted independent and detailed sampling within the tribe Miconieae (Melastomataceae), along the same gradient. Within Miconieae, I also measured functional leaf-traits associated with species resource-investment strategies, allowing investigation of the potential mechanistic processes underlying distribution trends across elevation.

I reveal a tendency for closely related woody plant lineages to occupy similar mean elevations and display phylogenetic clustering both above and below the cloud-base ecotone. A few exceptional lineages are able to occupy broad elevations, yet they are not each other's closest evolutionary relatives. I further show that, across both taxonomic and phylogenetic measures, the diversity of mid-elevation tropical montane forests may rival, or even exceed that found in the tropical lowlands, especially when the full evolutionary history of lineages is represented. Deviation among diversity measures is driven by variation in the evolutionary age structure of communities across elevation. Older evolutionary lineages are more numerous at middle to high elevations, while many evolutionarily younger lineages are restricted to distributions at lower elevation. Utilising Miconieae as a test lineage, I show that elevational diversity and distribution patterns at the species-level largely echo genus-level trends. Lastly, I reveal that closely related species tend to have similar functional leaf trait values, with certain traits displaying elevational trends. Amongst measured traits, only specific leaf area (SLA) appears to share an evolutionary correlation with species' elevational distributions. It may be that unmeasured traits or resource investment strategies unrelated to SLA, are more significant drivers of species constrained elevational distributions.

Overall, the work presented in this thesis adds to the body of evidence demonstrating that evolutionary factors, such as niche conservatism, form an important lens through which to understand the spatial organisation of biodiversity. I demonstrate that the broad relevance of evolutionary processes applies to woody plant distributions within unique and vulnerable tropical montane forests and may prove important to our understanding of the ecological response of this system to ongoing global environmental change.

Lay summary

The forests found on the flanks of tropical mountains contain levels of biodiversity that are globally important, including many species which are found nowhere else. These forests and species influence the vital water supply for millions of people around the world, and also interact with the global cycling of carbon. However, they are highly vulnerable under ongoing environmental change. A major part of understanding and protecting natural systems is knowing where species occur and why they occur there. Across tropical mountain forests, environmental conditions vary substantially, most notably in terms of temperature which decreases with increasing elevation. Multiple habitat types are found across elevation. A notable and iconic example is the unique cloud forests that occur above around 1500 to 2000 m asl. Within the context of this environmental variation, many tree species are only able to exist over very narrow elevations, often less than a hundred or so metres.

In this research, I focus on the distribution and diversity of trees within a forest spanning the Amazonian flank of the Peruvian Andes from 400 and 3600 metres above sea level. I use the lens of evolution to try and shed light on the causes of elevational patterns and changes in tree biodiversity. Understanding how evolutionary factors influence biodiversity distribution may prove vital in predicting how different species will respond to ongoing environmental change.

I show that middle elevations $\sim$1500 m asl in tropical mountain forests, may hold levels of biodiversity comparable with the more famously diverse tropical lowland forests of the Amazon. Moreover, if evolutionary history is given value in diversity calculations, these middle elevation forests may be even more important. Trees occuring at mid to high elevations tend to belong to evolutionarily older groupings, while many trees from evolutionarily younger groups are only found at lower elevations. Much of the tree diversity at middle and higher elevations may have had an evolutionary history seperated from that of trees at lower elevations. As such, these tropical mountain forests may be of unique and important conservation value.

Biologists group species based on evolutionary relationships. As brothers and sisters tend to be more similar to each other than they are to their cousins, and cousins tend to be more similar to each other than they are to more distant relatives, species and groups that are more closely related by evolution tend to be more similar to each other in terms of ecological characteristics. I find that groups of closely related trees tend to occur at similar elevations. Further, while most evolutionary groups tend to be found over very narrow elevational ranges, a few groups do not appear to play by the same rules and occur across nearly the whole elevational range of this forest. Part of this thesis makes a more detailed examination of one of these groups of tree species called the Miconieae.

Within the forests studied the Miconieae group contains $\sim$80 species that occur from low to high elevations. When looked at in detail I find that the exception proves the rule and as in larger groupings, closely related species in Miconieae also occur at similar elevations. I also find that closely related species tend to have similar leaf characteristics. Such characteristics can indicate whether a tree follows a 'live-fast, die young' or a 'slow and steady' ecological strategy. These leaf characteristics also vary predictably over elevation and the possession of certain leaf characteristics, such as leaf thickness, may have an evolutionary linked with the elevational environment a species is capable of existing in. Overall the work presented in this thesis contributes to a broader scientific literature showing that an evolutionary perspective is important for a full understanding of biodiversity distribution. Evolutionary factors hold important insight into the potential response of tropical mountain forests to ongoing environmental change.

Declaration

The plot census data utilised in analyses presented in chapters 2 and 3 belongs to the Andes Biodiversity and Ecosystem Research Group (ABERG) a collaborative project led by Miles Silman (Wake Forest University). The plot data is the product of a massive logistical effort, the work of many hands and many days in the field.

I declare that I composed this thesis. The work presented here is my own, except where otherwise acknowledged. This work has not been submitted, either whole or in part, for any other degree or professional qualification.

Andrew R. Griffiths
August 2019

Acknowledgements

In many senses my foremost gratitude is to the mountains for simply being there. A love of the peaks and fells has both guided and sustained me for many years. Rocks, ridges, a fascinating flora, and sense of adventure has long drawn me upwards. The world seems stripped to its core in the harshness of the higher places. Yet, among cold rocks and sharp peaks, life sneaks through in the cracks and crevices, clinging to an existence that exposes both the fragility and tenacity of nature. Elevation often provides perspective. Undertaking this doctorate afforded a privileged opportunity to explore a montane environment previously unknown to me. Not one of ice and rock and tiny alpine flowers, but one of tangled chaos, ethereal mists, and dripping, moss laden boughs. A truly otherworldly place overflowing with an intricate ecology.

In stories both modern and ancient, mountains feature as sites of pilgrimage and places to which people travel, seeking the wisdom of a sage or oracle. The wise man sat atop the tropical mountain of this thesis is my principal supervisor Kyle Dexter, to whom I address my greatest thanks. Kyle's patience and openness has smoothed over the many bumps that may otherwise have turned into insurmountable barriers. Under his guidance, my scientific skills have developed and I at last feel proud of what I have produced. My other supervisors have also provided valuable input from afar. Patrick Meir has provided useful input and thoughts on my writing, while Miles Silman went out of his way to meet me at the top of the elevation gradient that is at the centre of my research. I also thank my thesis examiners Jane Hill and Casey Ryan for an enjoyable discussion of my research.

Two field expeditions to Peru, in 2016 and 2017, formed a major part of my research. Knowing no Spanish, and having never travelled to South America prior to this doctorate, neither of these two journeys would have happened, or been a success, without the assistance of numerous people. Kyle Dexter and Maria-Camila Gomez helped me organise and translate paperwork prior to travel. Eric Cosio, Norma Salinas, and Aniceto Daza welcomed me in Lima and facilitated navigation of an idiosyn-

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Back in Edinburgh I have benefited from academic assistance at both the University and Botanic Gardens. The Dexter 'Lab Group' - more properly known as PLEEBS - provided a scientific rooting and foundation for discussions, acting as a reassuring environment to test ideas. I thank Kyle, Ricardo, Pedro, Flávia, John, Hatem, Galena and Lizzie, and the stream of happy Brazilian visitors Fernanda, Vanessa, Rafael, Poly, Erica, Natashi, and Bruno. A number of other University staff including Aidan Keane, Gail Jackson, Casey Ryan, Caroline Lehmann, Matt Bell, Ally Phillimore, Graham Walker and Arthur, have made my time at the University fuller

The days I spent working from the Royal Botanic Gardens Edinburgh provided a valuable contrast. Lesley Scott help process my collections into the Herbarium and David Harris helped persuade me to be confident about my species identifications and trust in reciprocal illumination. Michelle Hart, Laura Forrest, and Ruth Hollands kept me on course during lab work. They never turned me away when I gloomily turned up at their door after yet another failed PCR run. Also at RBGE, Toby, Tiina, Elspeth, Colin, Peter, Sandra, Scott and Agron have either provided advice or simply been a friendly face. I was also lucky to gain botanical experience and assistance further afield. I will be eternally grateful to Fabian Michelangeli at New York Botanic Garden

for welcoming me into his family home and spending time helping me puzzle over mystery vegetative specimens.

Beyond my academic pursuits, many friend and family are probably unaware of how much I have appreciated their many forms of companionship over the past four years. I am thankful for those who have provided an anchor to reality when the abstractions of academia became too much, and for those who provided an escape when writing a thesis became too much of a reality.

The office in the attic of the Crew Building has seen many come and go. Bay buddies Jack, Pippa, Claudia, and especially Anna (and Ellie) have been particularly important. Many other residents and members of the tea crew have made life up there fun; Robyn, Lettice, Jakob, Geoff, Pedro (my academic big brother), Paula, Kathleen, Sophie, Charlotte, Ebuka, Iain, Sandra, Mariana, Gill, Ben, and the regular crossword team Doug, Mark, Sam and Andy D. Special thanks are reserved for Doug and his kindness in giving me a shelter when the clouds hanging over the last months were at their darkest and most brooding.

I found a second home In the PhD offices down in the basement of the Botanic gardens, from my first visit when Karina, Julieth and Flávia – the 'South' American stars – were so bright, welcoming and happy to give me points. The friendships of Lucia, Mauricio, Surahbi, Andres, Pakkapol, Kristine, Yun-Yu, Jess, Hannah, Thibauld, Nadia, Isuru, Cynthia, Natalia, Subhani, have all helped me through. Most deeply I thank Flávia. Nossa! Maybe it would have never looked this pretty without her macumba. My debt is unpayable. Obrigado for the wandering, the wondering, and the enigmatic quest towards an unknown island. Let's go exploring!

Outside of the workplace, flatmates Will and Lucas have been through the furnace with me. I have also shared important time with Ribanna, John, Max, Lauren, Rob, Jake, Cathy, Ben, Eleri, Roseanne, Jack and Jan. My climbing friends Berta, Flávia, Mauricio, Sina, Tas, James, Alastair and Dave have shared my in my favourite distraction and made the times brighter. I especially thank Dave for continually tempting me

into finding harder ways up the mountain.

Those not based in Edinburgh have been equally important. I may never have embarked on this doctorate without the love, encouragement and support of Nicole, who helped me believe I was capable of such a thing. Du bleibst immer in meinem Herzen. To my parents and brother, so often under-acknowledged. The support and unconditional love of my family are the foundations that have allowed me the privilege of being able to follow my passions. My oldest friends from Brighton have also always been there, whatever nonsense has turned up along the way.

Finally, I want to acknowledge the generous financial support that has enabled me to spend four years pursuing the research presented in this thesis. NERC and the E3DTP provided me with a studentship to take on this doctorate. The Davis expedition fund and the generosity of Derek and Maureen Moss enabled me to complete field work in Peru. I thank Derek and Maureen for their interest in my research and support of environmental science in general. A grant from the Centenary Agroforestry Fund enabled my research visit to the New York Botanic Gardens.

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Chapter 1

Introduction

Determining where species occur, and understanding why they occur there, is at the core of ecology. With marked distribution patterns, such as high taxonomic turnover across elevation and exceptional levels of endemism, tropical montane forests (TMF) form one of the most biodiverse ecosystems on the planet (Myers et al., 2000). Yet these forests are particularly vulnerable under ongoing environmental change, with a high risk of substantial diversity losses (Feeley and Silman, 2010a,b). Much of the biota within tropical montane forests occupies narrow elevational ranges (Jankowski et al., 2013; Perez et al., 2016), and is unable to track expected temperature increases (Feeley and Silman, 2010b; Duque et al., 2015). Needing to adapt, acclimate, or face extinction (Aitken et al., 2008; Feeley et al., 2012), the response of tropical montane species to change remains poorly studied. Moreover, the growing recognition that evolutionary history can shape distribution patterns (Wiens and Donoghue, 2004; Mittelbach et al., 2007) has not yet been fully explored along tropical elevation gradients. Unravelling the role evolutionary constraints play in setting present day distribution trends may help predict responses into the future. Highly heterogeneous tropical montane forests, with variation in climate across elevation, provide an ideal natural laboratory in which to investigate distribution patterns across different environments (Körner, 2007; Malhi et al., 2010). The focus of this thesis is a study of woody plant distributions along an Amazon-to-Andes elevation gradient, with a particular emphasis on evolutionary trends and tendencies.

This introductory chapter provides the scientific background to my thesis. I first introduce the ecological interest in elevation in general and tropical montane environments in particular, along with the potential impacts of environmental change on this system. I then outline the development of an evolutionary perspective on spatial variation in biodiversity distribution patterns across different environments, followed by an overview of the relationship between functional traits and environment. A discussion of how ecological trends may vary across taxonomic and evolutionary scales then leads into an introduction to the plant tribe Miconieae, a focal lineage within this thesis. I conclude this chapter with an overview of the thesis, introducing the broad aims and

fundamental scientific questions addressed by the three empirical studies presented in Chapters 2 to 4.

1.1 Scientific background

1.1.1 The ecology of elevation

The montane environment holds an allure to ecologists that stretches back to the early days of explorer-naturalists and may be rooted in the many changes observable across elevation. In 1802 Alexander von Humboldt, Aimé Bonpland, Carlos Montúfar, and three guides, made a famous, yet ultimately unsuccessful attempt to summit the Ecuadorian volcano Chimborazo (6,263 m asl), believed at the time to be the worlds' tallest mountain. The principal motivation behind the expedition was to conduct scientific observations at different elevations, including measurements of temperature, pressure, air chemistry, humidity and the boiling point of water. Yet among the many studies made, those holding the greatest interest to future ecologists concerned the pattern of vegetation change with elevation (Humboldt and Bonpland, 1805; Morueta-Holme et al., 2015). A detailed record of plant distributions, along with the connected web of measurement made across the slopes of Chimborazo, was summarised and illustrated in von Humboldt's iconic Naturgemälde (Figure 1.1).

The spatial variation in environment associated with elevation provides a focus for ecological research. Across a gradient of elevation, many environmental factors display strong trends such as precipitation, solar radiation, atmospheric pressure, and land area (Körner, 2007). Amongst these myriad elevational patterns, temperature is frequently highlighted as the key elevational climate trend; perhaps regarded as particularly pertinent in light of increasing temperatures worldwide. Globally, the average adiabatic lapse rate for mountain regions is a temperature decrease of 0.55^{o}C for every 100 m gain in elevation (Körner, 2007), though there are degrees of diurnal, seasonal, and regional variation (Rapp and Silman, 2012). Such climatic variation, in combination with the heterogeneity of mountainous terrain, has great bearing on the

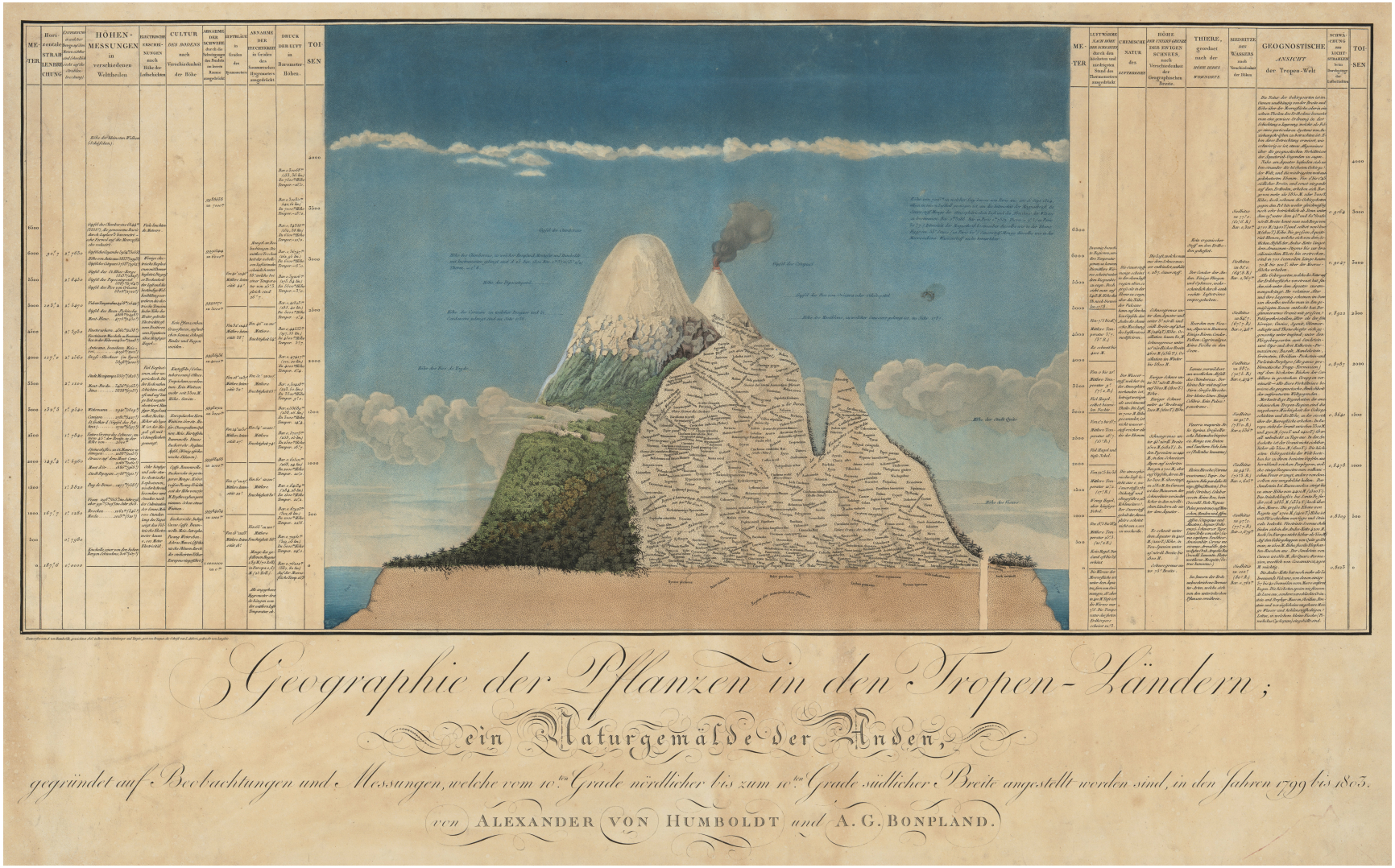

Figure 1.1: Alexander von Humboldt's Naturgemälde. A depiction of the Ecuadorian volcano Chimborazo in cross-section including detailed information of plant distributions and other scientific observations. First published in the 1805 *Essai sur la géographie des plantes as the Tableau physique des Andes et Pays voisins.*

flora and fauna, with substantial niche diversity found within a condensed geographic area. As such the montane biota provides great scope for investigating trends of distribution and adaptation.

Elevation gradients have gained attention as powerful natural laboratories for studying broad environmental drivers of ecological patterns and the response of ecosystems to global change (Becker et al., 2007; Körner, 2007; Malhi et al., 2010). Elevation has been leveraged for example, as an analog for latitudinal trends (Stevens, 1992; Qian and Ricklefs, 2016) and as a space-for-time substitution to studying climate change responses (Sundqvist et al., 2013; Read et al., 2014). While there is clear appeal to the use of elevation as a proxy system for multiple ecological phenomena, it is necessary to be circumspect in our generalisations. Some factors, such as atmospheric temperature and pressure, are closely tied to elevation, yet many factors displaying elevational trends, such as moisture, wind, and geology, are coincidental rather than elevation specific (Körner, 2007). While elevational trends are evidently interesting in their own right and can, when carefully considered, be of broader relevance, there is no standard mountain climate or structure. Under that light, it should be borne in mind that this thesis presents research conducted over a single tropical elevation gradient.

1.1.2 Tropical elevation gradients

Building upon the work of von Humboldt on Chimborazo, research along elevation gradients within tropical latitudes continues to generate important insights. The classic work of Janzen (1967), predicting that narrow physiological tolerances in tropical biota result in narrow elevational ranges and pronounced species turnover across elevation, spawned much discussion around physiological adaptation and distribution (Ghalambor et al., 2006). Terborgh's (1977) renowned bird studies along an Andean elevation gradient made a lasting impression on our understanding of diversity trends, creating a persistent belief in the linear decrease in diversity with elevation (Rahbek, 1995). More recently, large scale, multidisciplinary collaborations focusing on elevation gradients have made contributions across diverse themes. Some examples include plant

nutrient interactions in Ecuador (Báez and Homeier, 2018), the origins of endemism in Borneo (Merckx et al., 2015), insect diversity in Papua New Guinea (Leponce et al., 2016), and forest productivity variation in the Peruvian Andes (Malhi et al., 2017).

The variation inherent to long elevational gradients in the tropics is a core component of the Tropical Andes Biodiversity hotspot (Myers et al., 2000; Mittermeier et al., 2005), which with 45,000 plants - including 20,000 endemics - and 3,389 vertebrates, is the world's most species rich hotspot (Myers et al., 2000). Despite this globally exceptional diversity, the tropical Andes remain one of the most understudied regions in the world, particularly relative to their diversity (Stroud and Feeley, 2017). The elevation gradient that is the focus of this thesis lies on the eastern edge of the tropical Andes, representing a major environmental transition where the lowland forests of the Amazon meet the steep flanks of the Andean mountain chain. In terms of habitat change, this gradient represents a shift from lowland forests, through montane forest and up to the treeline-puna grassland transition, which typically occurs before 3700 m asl (Lutz et al., 2013) (Figure 1.2).

As with elevation globally, multiple abiotic and biotic trends are associated with elevational change across tropical montane forests. Perhaps the most significant elevational changes occur at the cloud-base ecotone (Fadrique et al., 2018), the transition from lower montane forest into tropical montane cloud forest (TMCF). This transition is associated with step changes in precipitation (Rapp and Silman, 2012), soil properties (Whitaker et al., 2014; Nottingham et al., 2015b) and solar radiation (Fyllas et al., 2017). A unique and enigmatic habitat, characterised by frequent and extended cloud immersion (Stadtmüller, 1987), tropical montane cloud forest and the significance of the cloud-base ecotone is a thread which runs through this thesis.

On the eastern side of the Andes, clouds form at the condensation point where north-easterly trade winds, transporting moisture from the tropical Atlantic are pushed upwards by the mountains and meet the cold, dry air of the high Andes (Rapp and Silman, 2012). Occurring above approximately 1500-2000 m asl, these Amazon facing

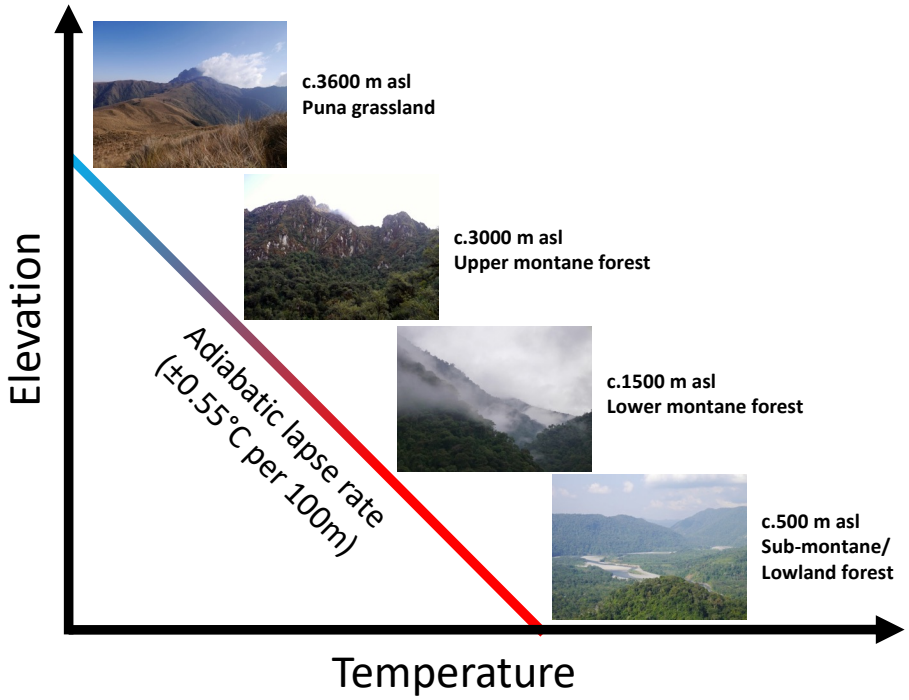

Figure 1.2: Conceptual illustration of the relationship between elevation and temperature, with photographs showing how type of habitat changes across a neotropical montane elevation gradient.

cloud forests are unusual in their location far from coastal systems (Rapp and Silman, 2012). A regular covering of clouds has numerous ecological consequences for the species which occur here. For example, cloud immersion results in a decrease in photosynthetically active radiation, but an increase in diffuse radiation (Moser et al., 2007). In addition TMCF species must adapt to high humidity and occult precipitation (Foster, 2001; Goldsmith et al., 2012). The environmental uniqueness of cloud forests has promoted exceptional levels of endemism (Foster, 2001), while many economically useful plant lineages are also found here. For example, Neotropical cloud forest may have been a global centre for the domestication of crop plants such as corn, beans, peppers and tobacco (Luna-Vega et al., 2001).

1.1.3 Environmental change and tropical montane forests

The accumulating research effort along tropical elevation gradients has facilitated the study of the temporal dimension that is so important for understanding how modern

environmental change may impact natural systems. Across the tropics, many organisms are moving upslope in response to increasing temperatures. To list but a few of the many examples, birds are moving upwards in Papua New Guinea (Freeman and Class Freeman, 2014), moths are moving upwards in Borneo (Chen et al., 2009), and trees are moving upwards in Peru (Feeley et al., 2011). The observations of von Humboldt have even been revisited, suggesting that more than 200 years after the famed expedition, vegetation zones have moved upward on the slopes of Chimborazo (Morueta-Holme et al., 2015). The movement of montane diversity to higher elevations in the tropics, is consistent with a global trend for upward and poleward range shifts in response to rising temperatures (Walther et al., 2005; Parmesan, 2006; Chen et al., 2011). Yet despite this apparent response, species may not be able to move fast enough to track predicted rates of climate warming (Feeley and Silman, 2010b; Corlett and Westcott, 2013; Duque et al., 2015). If migration is not sufficient, species must either adapt or acclimate, or they will likely face extinction (Aitken et al., 2008; Feeley et al., 2012).

The tropical biota is expected to be highly sensitive to environmental change (Bush et al., 2004; Colwell et al., 2008). The intrinsic stability of the tropical climate means species may not be adapted to large oscillations of climate in the manner of temperate species (Janzen, 1967; Ghalambor et al., 2006). This is particularly true for tropical montane regions where species exhibit a high degree of niche specialisation and restriction to narrow thermally regulated elevational bands (Jankowski et al., 2013; Perez et al., 2016), and it is anticipated that the climatic environment will change significantly (Feeley et al., 2011). Tropical montane forests face a number of particular threats associated to environmental change. The expected upslope movement of more competitive lowland species, may result in montane species suffering population reductions, while a downslope expansion of montane grassland - likely driven by human activities such as agricultural expansion (Morueta-Holme et al., 2015; Feeley and Rehm, 2015) - means montane forests are being squeezed from above and below.

Tropical montane cloud forests, among the most rare and vulnerable environments

on earth (Bruijnzeel et al., 2011), may be highly impacted by alterations to cloud dynamics. Warming ambient air temperature may raise the condensation height of cloud formation, thereby reducing the area of tropical montane cloud forest and altering the precipitation and humidity regime (Helmer et al., 2019). Such changes may also leave cloud forests more susceptible to fire (Mutke et al., 2017). More broadly, tropical montane forest provides important regulation of hydrological processes (Bruijnzeel et al., 2011) and influences carbon and nutrient cycling (Girardin et al., 2010; Spracklen and Righelato, 2014; van de Weg et al., 2014). Such ecosystem services may be severely impacted if ongoing environmental change substantially alters tropical montane forest systems.

1.1.4 An Amazon to Andes elevation gradient and the Andes Biodiversity and Ecosystem Research Group

The research presented in this thesis is based along a single, large elevation gradient on the Amazonian flank of the Peruvian Andes stretching from 425 to 3625 m asl and centred around Kosñipata valley, both in and near Manu National Park, south-eastern Peru (Figure 1.3). The core research component of this elevation gradient is a network of one-hectare forest inventory plots, established and maintained by the Andes Biodiversity and Ecosystem Research Group (ABERG: www.andesconservation.org). The elevation gradient encompasses broad variation in habitat and environment, from lowland/sub-montane forests below 800 m asl, up to the montane forest-puna grassland transition at c.3400 m asl (Girardin et al. 2010, Figure 1.2). Forest physiognomy changes across the gradient, with greater canopy gap occurence and a reduction in tree stature with increased elevation (Asner et al., 2013).

Across the gradient mean annual temperature decreases from c.24^{o}C at low elevations, to c.9^{o}C at higher elevation, with little annual variation (Rapp and Silman, 2012; Malhi et al., 2017). Temperature declines with a mean adiabatic lapse rate of 0.52^{o}C every 100 m of elevation (Rapp, 2010). Mean total annual precipitation displays a hump shaped trend across the gradient, ranging from c.3000 mm yr^{1} at low

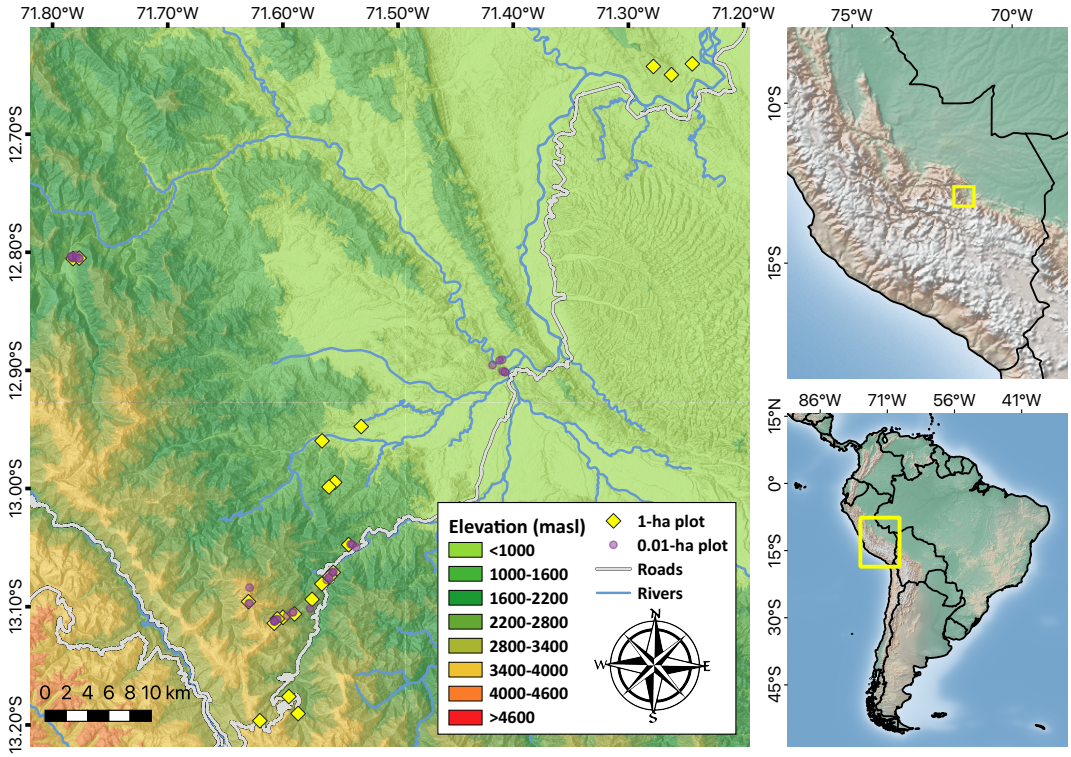

Figure 1.3: Map showing the location of the tropical montane forest elevation gradient on the Amazonian flank of the Andes in south-eastern Peru. Yellow diamonds indicate the location of 1-ha plots analysed in Chapters 2 and 3. Purple circles indicate 0.01-ha plot focused on in Chapter 4.

elevations to c.5000 mm yr^1 at mid elevations and c.1000 mm yr^1 at high elevations (Rapp and Silman, 2012). Precipitation displays annual variation with highest rainfall in January/February and lowest rainfall in June/July. Annual wind patterns show limited variation with patterns largely determinded by terrain and diurnal rotation of upslope and downslope air movement (Rapp and Silman, 2012). Cloud immersion frequently occurs above c.1500-2000 m asl (Girardin et al., 2010; Rapp and Silman, 2012).

In terms of geological character, the gradient is predominantly underlain by Ordovician shales and slates (Salas et al., 1998) with plutonic granite intrusion between 1500-2000 m asl (Nottingham et al., 2018). Soils characteristics change from Haplic Allisols and Haplic Cambisols below 1000 m asl, to Cambisols between 1000-2020 m asl, and Umbrisols above 2520 m asl (Nottingham et al., 2018). The highest levels of soil carbon, nitrogen, and phosphorus are found between 2000-3025 m asl, where a thick layer of humic material occurs, with depths of around 30 cm (Girardin et al., 2010). However, in general nutrient availability decreases with elevation, caused in part by a reduction in the rate of decomposition processes at lower temperatures (Nottingham et al., 2015b). Soil processes may also be limited by moisture extremes such as poor retention in the shallow soils of steep slopes, or water-logging (Zimmermann et al., 2010).

Although the elevation gradient encompasses primary montane forest, the environment is unlikely to have completely escaped the influence from human activity. Indeed, it has been shown that across the Amazon, forest inventory plots are located disproportionately near areas likely to have experienced ancient human impacts (McMichael et al., 2017). The main ridge line on which plots are located contains a trail that is speculated to have been in use since at least the Incan era. While the high elevation puna-grassland habitat has a history of use as grazing land, though cattle have been removed in recent years.

Census data for the network of one-hectare plots forms the basis for the analyses presented in chapters 2 and 3 of this thesis. These data record and identify all living

woody stems >10cm diameter at breast height (DBH = 1.3m), representing true trees, pteridophyte tree ferns, palms, and lianas. Chapter 4 presents novel sampling of 0.1-hectare plots along the same gradient, and records woody stems >1cm DBH. The 0.1-hectare plot sampling represents relatively fewer emergent canopy trees and may be more representative of ecological trends in the understory than the one-hectare plot data. In both plot sets, plots are seperated by approximately 250 m of elevation. Many plots are located on steep ground on or near a ridge line running in a easterly to north-easterly direction. Further plots are located on the relatively flatter ground towards the base of the mountains.

In highly diverse and heterogeneous environments, such as tropical montane forests, the accurate estimation of diversity and distribution trends is complex and it is likely that rare species are frequently underrepresented (Hopkins, 2007; Schulman et al., 2007). For the majority of the plots along this elevation gradient, species accumulation curves do not converge on a horizontal asymptote (Figure 1.4), suggesting incomplete sampling at the species-level. As such it is likely that species diversity and range estimates derived from these plot data are conservative. Given chapters 2 and 3 of this thesis focus on patterns at the genus-level this species-level undersampling is likely to be less of an analytical issue. Nevertheless the context of conservative diversity and range estimates should be considered across the analyses presented in this thesis.

The ABERG project is an inter-disciplinary and cross-institutional collaboration. To date the research group has published over 100 papers across paleoecology, climate science, ecosystem and distributional ecology, advancing the understanding of biodiversity and ecosystem function, and the effects of climate and anthropogenic change in the Peruvian Andes (Malhi et al., 2010, 2017). Along this elevation gradient, it has been demonstrated that tropical tree distributions are moving upslope. However, mean migration rates of c.2.5 m a year are insufficient to track predicted warming trends (Feeley et al., 2011). Further investigation has shown that while directional shifts in distributions and species abundances are widespread across the tropical Andes, they are not uniform across elevation. Variation is likely caused by different warming rates

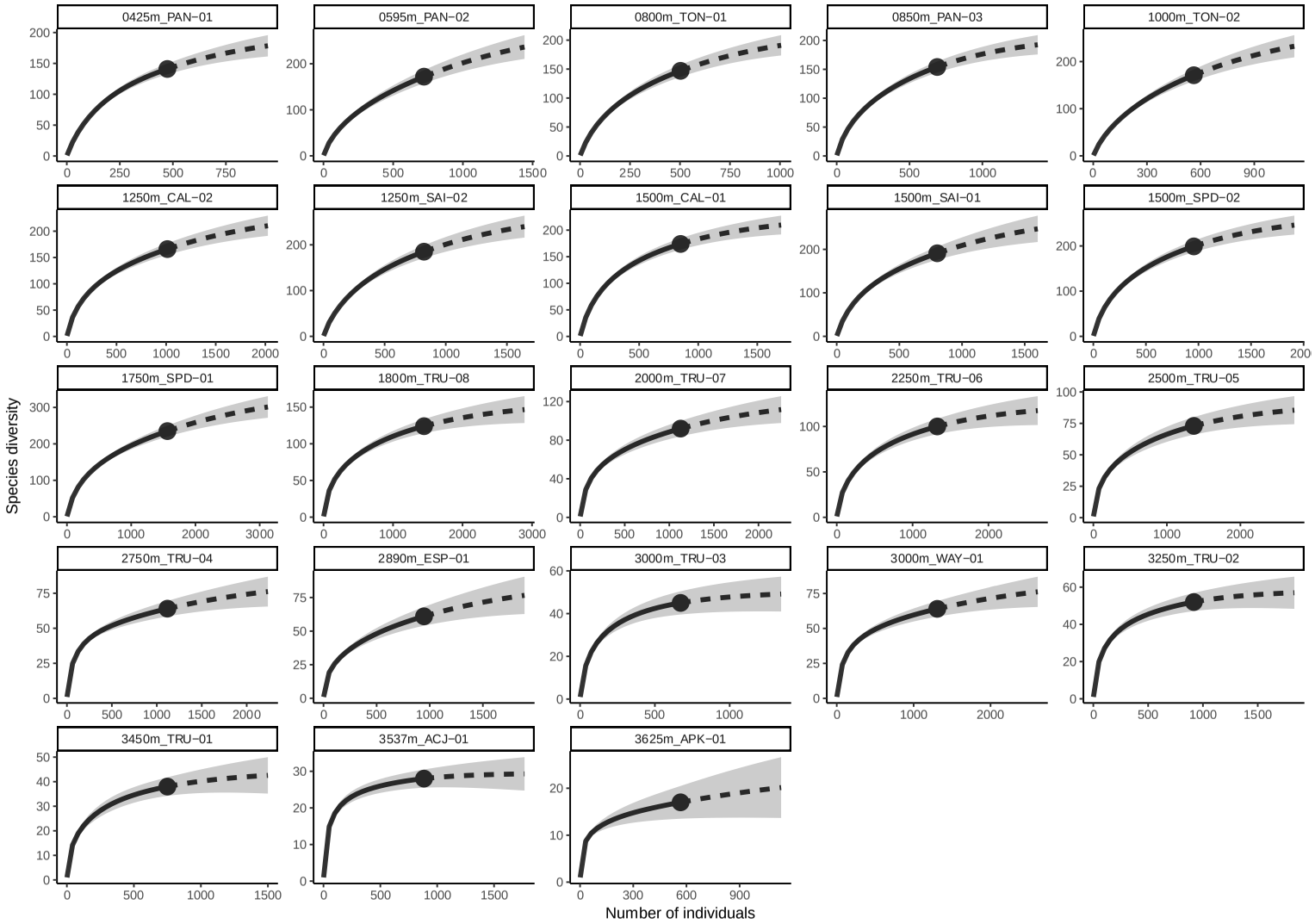

Figure 1.4: Species accumulation curves for each one-hectare plot in the ABERG network, based on the number of individuals sampled. Solid circles indicate the observed number of species in each plot. Solid lines represent interpolated diversity. Dashed lines represent extrapolated diversity. Shaded areas represent standard error.

across elevation and the presence of specialised tree communities at ecotonal transitions such as the treeline or cloud-base (Fadrique et al., 2018). Indeed, moisture availability, regulated by cloud cover, has been shown to be the most significant factor driving montane forest change in paleo-ecological history (Urrego et al., 2010).

Work along this tropical montane forest gradient has also shown elevational patterns of variation in forest structure and productivity, functional traits, and biotic interactions. Declines in tree height and above-ground wood biomass, and increases in stem density, occur with increasing elevation (Girardin et al., 2014), while decreased rate of tree growth has been observed at higher elevations (Rapp and Silman, 2012). Gross-primary productivity of tropical montane cloud forest, driven by temperature, is lower than that of the lowland Amazon (van de Weg et al., 2014), and a trend of decreasing net primary productivity is seen with increased elevation (Girardin et al., 2010, 2014; Malhi et al., 2017). Conservative leaf trait strategies increase with elevation. For example leaf mass per area (LMA) and leaf nitrogen by area increase by c.50% from lowland to montane sites (van de Weg et al., 2009; Bahar et al., 2017). Additionally, within montane forests soil microbes possess traits which increase their nitrogen uptake (Nottingham et al., 2015a). Lastly, above around 1000-1500m biotic interaction pressures such as seed predation and herbivory have been shown to decrease (Hillyer and Silman, 2010; Rapp et al., 2012).

Much of the research outlined above fits within one of the key research themes of the ABERG project: to understand the interaction between climate and plant diversity distributions, past, present, and future. However, as of yet little focus has been given to an evolutionary perspective on ecological trends across this elevation gradient. This thesis aims to address that knowledge gap.

1.1.5 Towards an evolutionary perspective on spatial distribution patterns

Historically, efforts to understand the drivers of spatial variation in diversity and distribution patterns have tended towards an environmental and ecological focus (Waide et al., 1999; Francis and Currie, 2003; Willig et al., 2003). For example, environmental correlations are often cited in discussions of the latitudinal diversity gradient, the trend of decreasing diversity with latitude away from the tropics (Currie, 1991; Currie et al., 2004; Kreft and Jetz, 2007). However, attention to an evolutionary perspective on diversity and distribution patterns has increased (Faith, 1992; Wiens and Donoghue, 2004; Mittelbach et al., 2007).

The evaluation of evolutionary factors has been formalised in approaches such as the phylogenetic comparative method, which utilises information about evolutionary relationships among taxa as a way of understanding the patterns and processes underlying ecological trends. Such comparative approaches have a long history, even if not in a formal statistical sense. For example, the differences and similarities between species underpinned many of the ideas presented in Darwin's On the Origin of Species (1859). However, modern ecology's interest in an evolutionary perspective can be traced back to the development of molecular phylogenetics - the practice of comparing genetic sequences to infer evolutionary relationships (Zuckerkandl and Pauling, 1965) - and the increasingly attainable production of robust phylogenetic trees (Baum and Smith, 2013). Methodologies for using phylogenetic information were developed in a number of seminal papers. Felsenstein (1985) clearly communicated, and provided solutions to, the problem of assuming that individual taxa constitute statistically independent units. Faith (1992) integrated evolution into conservation evaluations by developing a quantification of evolutionary diversity using phylogenies. Webb (2000) used an example of tropical rainforest trees to demonstrate the importance of phylogenetic relationships in shaping the structure of ecological communities.

A significant evolutionary trend thought to have implications for ecological pat-

terns and processes is phylogenetic niche conservatism (PNC; Wiens and Graham 2005. Prominent within this thesis, PNC can essentially be seen as the tendency for evolutionary lineages to retain their ancestral characteristics (Harvey and Pagel, 1991; Wiens et al., 2010). The evolutionary lineage is a fundamental biological concept, defined as a group of organisms connected by ancestor-descendant relationships (De Queiroz, 1998). Analytical efforts to measure and quantify the influence of evolutionary heritage on present-day ecological characteristics of lineages have pursued multiple approaches, including metrics focusing on the more specific concept of phylogenetic signal (Blomberg and Garland, 2002; Losos, 2008; Münkemüller et al., 2013). Blomberg and Garland (2002) defined phylogenetic signal as *"a tendency for related species to resemble each other more than they resemble species drawn at random from a tree"*, and synthetic tests of phylogenetic signal, such as Moran's I Index (Moran, 1950; Gittleman and Kot, 1990), Pagel's λ (Pagel, 1999; Freckleton et al., 2002), Blomberg's K (Blomberg and Garland, 2002), test for the statistical significance of the pattern.

Phylogenetic niche conservatism, phylogenetic signal, and a general evolutionary perspective are considered throughout this thesis. A growing quantity of research has focused on how evolutionary history may constrain and limit distribution patterns. One explanation of the latitudinal diversity gradient is based on the assumptions that most lineages evolved in, and are constrained to tropical climates. Given evolutionary shifts away from an ancestral tropical niche into temperate latitudes are uncommon, diversity will be lower at higher latitudes (Wiens and Donoghue, 2004). If the ancestral niche determines the distribution and environmental tolerances of lineages, evolutionary heritage may provide essential insight into our understanding of whether species will be able to persist in the face of environmental change (Wiens and Donoghue, 2004). In the context of tropical montane forest, elevational patterns of complete species turnover and narrow ranges are well known (Malhi et al., 2010; Jankowski et al., 2013; Perez et al., 2016), yet whether these patterns are shaped by evolutionary factors is unclear. The evolutionary trends and tendencies potentially shaping the distribution

and diversity of woody plant lineages within TMF are the central focus of this thesis (Figure 1.5).

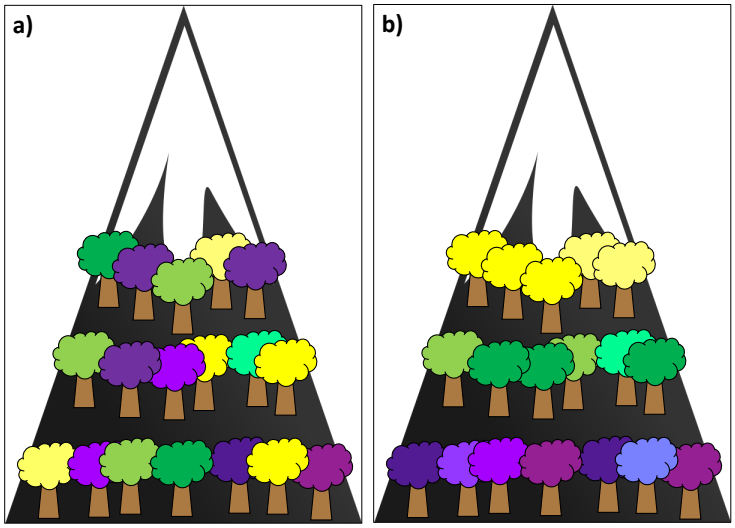

Figure 1.5: Conceptual illustration of elevational distributions in different evolutionary lineages. Each colour represents an evolutionary lineage, with shading representing individual taxa. Panels illustrate potential scenarios where **a)** taxa within an evolutionary lineage occur across elevations without evolutionary constraint and **b)** all taxa within an evolutionary lineage occur at the same elevation, constrained by evolution. If environmental change substantially alters forests at high elevation for example, in scenario b) the whole evolutionary history and diversity of the yellow lineage might be lost.

1.1.6 Functional traits across environments

Much of the early work highlighting the association of ecological patterns with phylogenetic relationships centred on traits. A seminal example demonstrated that the apparent correlation between brain weight and body size in mammals (Martin, 1981) may in reality be a result of closely related species sharing similar traits (Felsenstein, 1985). More recently, functional traits have gained an important role across ecology, being considered by some as providing the 'holy grail' for understanding ecological processes (Lavorel and Garnier, 2002). In terms of understanding distribution patterns, functional traits certainly have utility in bringing a physiological underpinning to interpretations, and the potential to provide a mechanistic explanation for patterns. For plants, the relationship between traits and ecological strategies has been formalised

in the global leaf economic spectrum (LES; Wright et al. 2004). The LES allows one to measure simple predictor traits, such as specific leaf area (SLA), which are then placed in the context of a spectrum of resource investment, such that low SLA values for example, are indicative of a resource conservative ecological strategy, while high SLA values indicate resource-acquisitive strategies. Further, traits, and consequently ecological strategies, have been convincingly shown to vary among species and across environments (Reich, 2014; Read et al., 2014).

Within tropical plants it has been demonstrated that many functional traits, such as leaf structure, wood density, seed mass, tree size, and growth rate (Baraloto et al., 2012; Yang et al., 2014; Coelho de Souza et al., 2016), display phylogenetic signal and are thus likely influenced by evolutionary processes. Understanding potential evolutionary association and constraint of functional trait trends within tropical montane forests species may provide a mechanistic understanding for elevational distribution patterns. In addition, quantification of trait patterns may provide insight into potential responses of the tropical montane system to environmental change. For example, within tropical montane cloud forest, a reduction in cloud immersion and rainfall, and an increase in temperature, may push the functional nature of the plant community towards faster-growing, resource-acquisitive species (Helmer et al., 2019).

1.1.7 Trends across taxonomic and evolutionary scales

Establishing whether ecological patterns and trends hold as tractable and generalisable rules has been a long-term goal within ecology (Levin, 1992; Rapacciuolo and Blois, 2019; McGill, 2019). However patterns are often contingent on the scale of study, be it spatial, temporal, or taxonomic (Levin, 1992; Simberloff, 2004; Vellend, 2010). The influence of temporal or evolutionary scale may affect for example, our interpretation of diversity patterns. Our understanding of the distribution of evolutionary diversity across environments may vary dependent on phylogenetic depth considered (Dexter et al., 2019). Problems of taxonomic scale are frequently encountered in tropical systems. The challenges of species identification, especially of vegetative plant

material (Dexter et al., 2010; Baker et al., 2017) often results in analyses being conducted at the genus-level (Coelho de Souza et al., 2016; Esquivel-Muelbert et al., 2017). However, it has been demonstrated that genus-level data and analyses can be misleading (Smith and O'Meara, 2009). Species level analyses may enable the validation of many patterns observed at higher taxonomic scales. Moreover, in terms of understanding evolutionary patterns, species are the unit at which many evolutionary processes are considered to operate, while higher taxonomic classifications such as genus and family, suffer from being largely arbitrary groupings (Sigwart et al., 2018).

Additionally, and despite its difficulty, detailed species level work involving named identifications can provide valuable biodiversity information, especially in the tropics where many species and their distributions remain undiscovered and unknown. Within this thesis, I seek to first investigate genus-level patterns and then establish whether they hold at the species-level. During the genus-level analyses of Chapter 2 and Chapter 3, one particular lineage, *Miconia*, revealed itself as exceptional in its diversity, abundance, and elevational range (Figure 1.6), and thereby provides an ideal test lineage in which to identify whether genus level trends are echoed at the species-level.

1.1.8 *Miconia*, Miconieae, Melastomataceae

Miconia Ruiz & Pavón, is the largest genus within the family Melastomataceae. With more than 1050 species it is one of the largest genera of flowering plants, and perhaps the largest that is exclusively Neotropical in its native distribution (Michelangeli et al., 2004). Predominantly shrubs and small trees (Goldenberg et al., 2008), some *Miconia* are vines, hemi-epiphytes, or epiphytic shrubs, and a few are large trees (Wurdack et al., 1993). Often found in very moist, hilly, and forested habitats (Ruokolainen et al., 1997), *Miconia* is distributed from western Mexico and the Caribbean to Uruguay and northern Argentina, occurring from sea level up to the Andean paramos (Goldenberg et al., 2008). Many species produce fleshy berries, an ecologically important food resource for the fauna of tropical and subtropical forests (Magnusson and Sanaiotti, 1987; Stiles and Rosselli, 1993; De Figueiredo and Longatti, 1997).

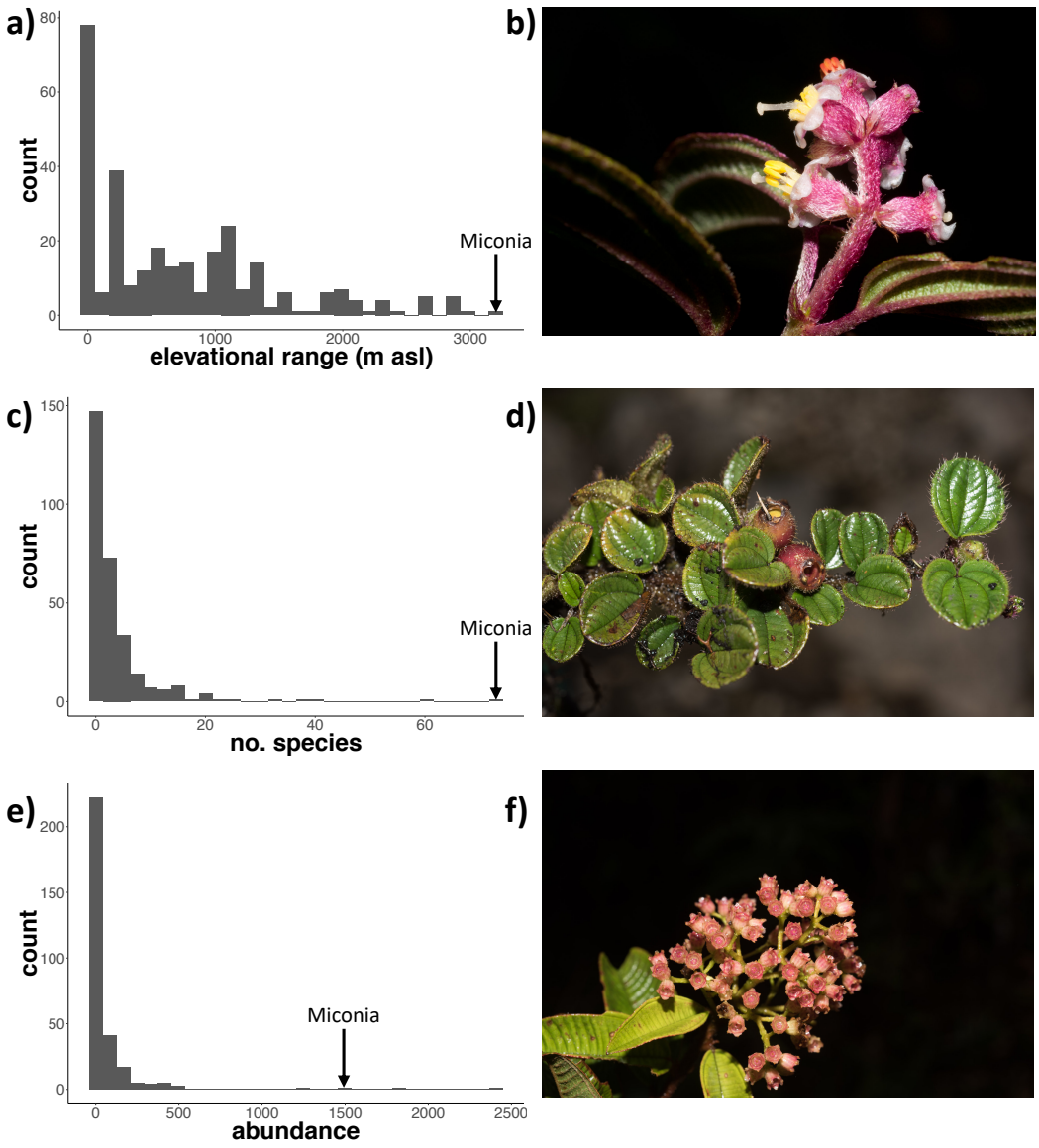

Figure 1.6: *Miconia* is exceptional among the tree genera along a tropical montane forest elevation gradient. Histograms demonstrate that amongst genera, *Miconia* has a) the broadest elevational range (= 3200m), c) the greatest number of species (n = 71), and e) the third highest abundance (n = 1530). b) *Miconia polytopica*, d) *Miconia rotundifolia*, f) *Miconia nigricans*. Photographs courtesy of Fabian Micheangeli.

Several species of *Miconia* have gained wider renown as invasive species. For example, *Miconia calvescens* is considered one of the most destructive invaders of island tropical rainforest, having gained the epithets of 'green cancer' of Tahiti, and 'purple plague' of Hawaii (Burnett et al., 2007). Ecologically, the broader Melastomataceae family is significant as an abundant, and often dominant contributor to the diversity of tropical montane forests (Gentry, 1988; Homeier et al., 2010). Further, among the tree genera of Amazonian forests, Melastomataceae may be exceptional within Rosid lineages in having a high species richness, yet low mean range size and mean abundance of genera (Dexter and Chave, 2016).

Historically, the taxonomy of Melastomataceae has proved complicated, with circumscription of many intra-familial relationships debated (Michelangeli et al., 2004). *Miconia* has been recognised as a paraphyletic genus (Judd and Skean, 1991; Michelangeli et al., 2004). Many other genera, such as *Clidemia* and *Tococa* are embedded within *Miconia*, meaning a given species of *Miconia* may be more closely related to a *Clidemia* species than other *Miconia* species. However, the tribe Miconieae sensu stricto, i.e. excluding the genera *Henriettea*, *Henriettella*, *Loreya*, and *Bellucia* is considered to form a monophyletic group comprising more than 1900 species assigned to 16-19 genera (Michelangeli et al., 2004; Goldenberg et al., 2008). Taxonomic work is ongoing in the group, with recent nomenclatural changes to many species reflecting a move to recognise *Miconia* as the sole genus within Miconieae (Michelangeli et al., 2019).

For the purposes of this thesis we utilise Miconieae sensu stricto, as described by Michelangeli et al. (2004), in order to focus on a monophyletic clade for evolutionary analyses. Despite its incredible diversity, Miconieae is a relatively understudied lineage with regular new discoveries and descriptions (Meirelles et al., 2015; Michelangeli and Goldenberg, 2016; Palacios et al., 2018). Indeed, two new species have recently been described from the elevation gradient that is the focus of this thesis (Burke and Michelangeli, 2018).

1.2 Thesis overview

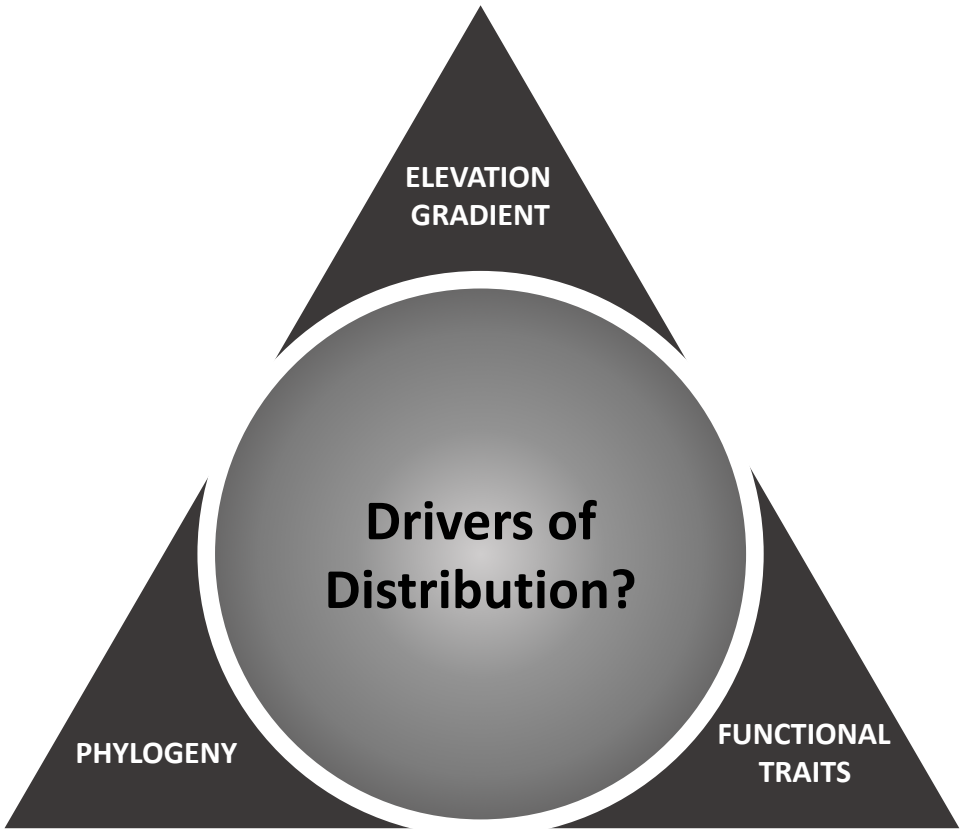

Figure 1.7: Conceptual illustration of the core components of research presented in this thesis.

1.2.1 Thesis aims

The overarching purpose of this thesis is to contribute towards an understanding of the role evolutionary constraint plays in shaping the elevational distribution and diversity patterns of woody plants within tropical montane forest. Tropical montane forests are home to numerous rare species, many of which are likely still to be discovered. However, current environmental change leaves the unique diversity of tropical montane forests in general, and tropical montane cloud forests in particular, highly vulnerable. A deeper understanding of the distribution patterns within tropical montane forests is essential if we are to understand the response of this distinctive system to environmental change. The patterns of taxonomic turnover and narrow elevational ranges

common within tropical montane forest are well known (Malhi et al., 2010; Perez et al., 2016), yet the role evolutionary processes play in setting these trends remains unclear. Pursuing both whole community level work at the genus-level and more detailed and focused analysis of the tribe Miconieae, I hope to gain generalisable insight into woody plant distribution trends. Utilising phylogenetic methods, leveraging the environmental variation of a tropical elevation gradient, and integrating functional trait measurements, this thesis ultimately aims to address the question of whether evolutionary constraint shapes the elevational distributions of tropical montane forest taxa (Figure 1.7). Specifically, this thesis aims to address the following core questions:

1. **Does evolutionary history influence the elevational distribution of woody plant taxa?**
2. **Does evolutionary history shape patterns of evolutionary diversity and richness over elevation?**
3. **Are elevational distribution and diversity trends consistent across evolutionary scales?**
4. **Do functional trait trends have an evolutionary association with species' elevational distributions?**

This thesis is composed of three empirical chapters each investigating a subset of these questions (Figure 1.8).

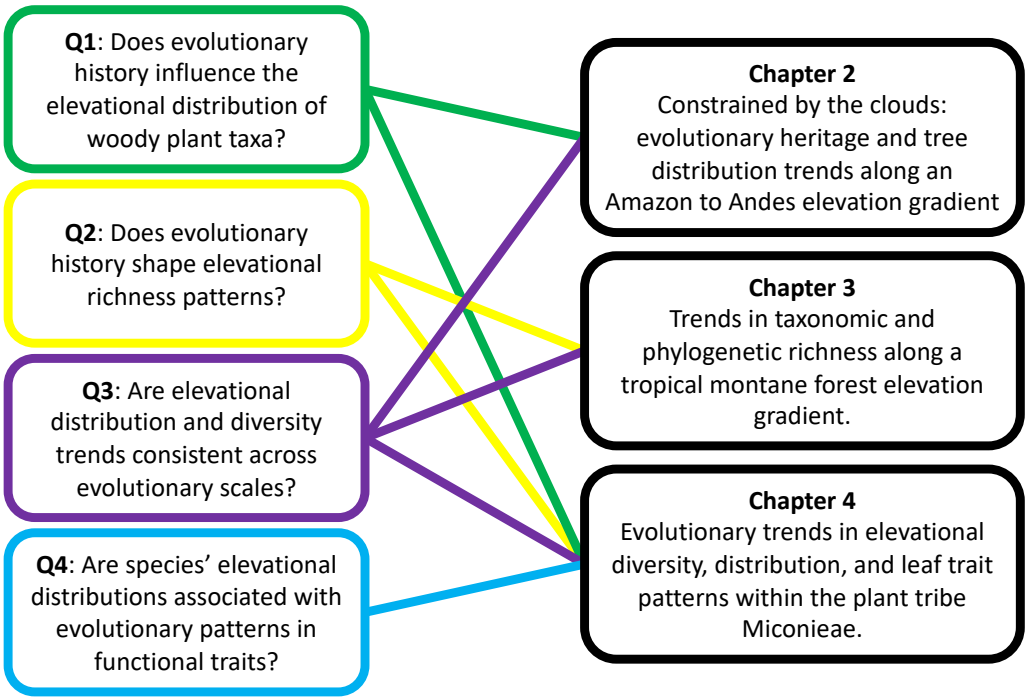

Figure 1.8: Conceptual illustration of the links between the four core science questions of this thesis and the three empirical chapters which address them.

1.2.2 Thesis structure

Chapter 2 - Constrained by the clouds: evolutionary heritage and tree distribution trends along an Amazon to Andes elevation gradient.

A study of potential evolutionary constraint on the elevational distribution of tree genera representing a breadth of vascular plant diversity from angiosperms and gymnosperms to pteridophyte tree ferns. The hypotheses that closely related genera occupy similar elevations, and that genera with potential evolutionary lability under environmental change are phylogenetically clustered, are tested. The significance of the cloud-base ecotone to the distribution patterns of different lineages is also considered.

Chapter 3 - Trends in taxonomic and phylogenetic richness along a tropical montane forest elevation gradient.

A genus-level examination of the nature of the elevational diversity gradient within tropical montane forest. A comparison of taxonomic and phylogenetic measures of richness is made as well as a deeper consideration of how the evolutionary age structure of plant communities varies across elevation within tropical montane forest.

Chapter 4 - Evolutionary trends in elevational diversity, distribution, and leaf trait patterns within the plant tribe Miconieae.

A species-level study of the plant tribe Miconieae examining whether general distribution and diversity patterns are reflected at the scale of species. Elevational and evolutionary patterns in functional leaf traits are also investigated with the aim of investigating potential mechanistic associations between leaf trait trends and elevational distributions.

Chapter 5 - Synthesis and Conclusions

A summary and synthesis of the key findings from Chapters 2 to 4, placed in the context of the core scientific questions addressed by this thesis. The wider implications of this research are considered, particularly under the spectre of ongoing environmental change, with suggestions for future research to develop on the results of the work presented here. The chapter, and thesis, ends with some concluding remarks.

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Chapter 2

Evolutionary heritage and tree distribution trends along an Amazon to Andes elevation gradient.

Work in this chapter is based upon the manuscript submitted as: “Evolutionary heritage and tree distribution trends along an Amazon to Andes elevation gradient”. Andy R. Griffiths, Miles Silman, William Farfan Rios, Kenneth J. Feeley, Karina Garcia Cabrera, Patrick Meir, Norma Salinas, Kyle G. Dexter; *Biotropica* (2020, in review).

2.1 Abstract

Understanding how evolutionary heritage influences the elevational distribution of tree lineages provides insight into the future of tropical montane forests under global change. With narrow elevational ranges, high taxonomic turnover, habitat specialisation, and exceptional levels of endemism, tropical montane forests and thier biodiversity are predicted to be susceptible to declines in adunbance and possible extinctions resulting from environmental change. Using plot census data from a gradient traversing more than 3000 m in elevation on the Amazonian flank of the Peruvian Andes, we employ phylogenetic approaches to explore distribution trends of tree lineages at the genus level. We reveal phylogenetic signal for elevational distribution, demonstrating a tendency for closely related lineages to occur at similar elevations. The mean elevational difference in distribution of sister genera pairs is 252 m lower than the difference between non-sister genera pairs. We also demonstrate phylogenetic clustering both above and below the cloud-base ecotone. Belying these general trends, some lineages occur across many different elevations. However, these plastic lineages are not phylogenetically clustered. Overall, our findings suggest that many tropical montane forest lineages, with elevational distributions constrained by evolutionary heritage, may struggle to adapt to environmental change.

2.2 Introduction

Ongoing global climate change underscores the need to examine evolutionary patterns underlying biodiversity distributions and potential evolutionary constraints limiting the response of biota to novel environmental conditions (Lavergne et al., 2012; Christmas et al., 2016). Closely related lineages frequently display similarities in ecological niche, functional characteristics (Felsenstein, 1985; Harvey and Pagel, 1991; Losos, 2008) and occupy similar environments (Wiens and Graham, 2005; Holt, 2009). Closely related lineages also tend to respond similarly to changing environmental conditions (Edwards and Donoghue, 2013). Understanding how evolutionary heritage

shapes distribution trends may provide a powerful tool for predicting the impacts of climate change - especially in highly diverse and poorly studied areas such as tropical montane forests.

Tropical mountains are globally exceptional in their biodiversity and levels of endemism (Hughes and Eastwood, 2006; Merckx et al., 2015). The mountains of the tropical Andes in particular are recognised as the most species rich of global biodiversity hotspots (Myers et al., 2000). Tropical montane forests (TMF) provide many ecosystem services, such as regulating hydrological processes (Bruijnzeel et al., 2011) and influencing carbon and nutrient cycling (Girardin et al., 2010; Spracklen and Righelato, 2014; van de Weg et al., 2014). However, tropical montane systems are experiencing rapidly increasing temperatures (Pepin and Mountain Research Initiative EDW Working Group, 2015; Russell et al., 2017) coupled with changes in precipitation regimes (Hu and Riveros-Iregui, 2016). The response of TMF to these changes remains poorly studied, yet given many TMF species are highly specialized and have narrow elevational ranges (Perez et al., 2016), there is a high risk of substantial diversity loss under significant climate change (Feeley and Silman, 2010a,b).

TMF is characterised by topographic complexity allied to cool, aseasonal temperatures (Grubb, 1977; Rapp and Silman, 2012) that decrease with elevation (Schimper, 1903; Koerner, 2007). Variation in precipitation, soil structure and biotic interactions across elevations also contribute to the unique character of TMF (Hillyer and Silman, 2010; Rapp and Silman, 2012; Nottingham et al., 2018). In addition to general elevational trends, certain distinct environmental shifts result in areas of TMF with markedly different conditions, such as the Tropical Montane Cloud Forest (TMCF), defined by almost constant clßoud immersion (Foster, 2001; Halladay et al., 2012). The mid-elevation transition from lower montane rainforest into TMCF, at the cloud-base ecotone, is one of the most evident changes in tropical montane ecosystems (Bruijnzeel, 2001; Fadrique et al., 2018) and is accompanied by significant environmental shifts in, for example, precipitation (Rapp and Silman, 2012), soil properties (Whitaker et al., 2014; Nottingham et al., 2015) and solar radiation (Fyllas et al., 2017).

The highly heterogeneous environment of TMF, along with specific elevational transitions, form a key driver of this system's exceptional biodiversity (Richter et al., 2009). The variation in environmental conditions across elevation, in combination with different climatic tolerances among species, manifests as notable changes in the vegetation community as one moves up mountain slopes (Humboldt and Bonpland, 1805; Grubb and Whitmore, 1966; Martin et al., 2011; Jankowski et al., 2013). Such elevational patterns may in part be explained by environmental filtering - i.e., the capacity for key factors, such as temperature, to act as a 'sieve' limiting the composition of communities to species with appropriate tolerances to local conditions (Kraft et al., 2015). Environmental filtering is thought to exert a stronger influence in harsher environments (Chase, 2007), such as the high elevations of montane systems (Marx et al., 2017).

Environmental tolerances may be constrained by evolutionary history, as posited by the concept of niche conservatism, which holds that colonisation and adaptation to novel environments is relatively uncommon (Wiens and Donoghue, 2004; Wiens et al., 2010). If niche conservatism interacts with environmental filtering, it is expected that evolutionarily close relatives will be clustered in similar environments (Cavender-Bares et al., 2009). Across the heterogeneous environment of the montane landscape, phylogenetic clustering at high elevations has been found among microbes (Wang et al., 2012; Nottingham et al., 2018), ants (Machac et al., 2011), ferns (Kluge and Kessler, 2011), and alpine plants (Li et al., 2014). Within TMF, tree communities at different elevations display significant dissimilarity in phylogenetic composition (Ramírez et al., 2019), with some plant lineages constrained to certain elevations or habitats such as TMCF. In the tropical Andes, species within genera such as *Weinmannia* (Cunoniaceae) and *Polylepis* (Rosaceae) tend to occur at higher elevations, while species within genera such as *Inga* (Fabaceae) and *Protium* (Burseraceae) tend to occur at lower elevations. However, the general strength of evolutionary constraints on elevational distribution across lineages, and at deeper evolutionary levels, is less clear. Tropical mountains are 'warming hotspots' (Bradley et al., 2009; Russell et al., 2017) and clarifying the influence of evolutionary heritage on the distribution of TMF tree lin-

eages and their responses to environmental change is important to our understanding of current and future biodiversity patterns in this unique system.

Under a rapidly changing environment, biota must either adapt, acclimate, migrate or face extinction (Aitken et al., 2008; Feeley et al., 2011). With rates of migration that seem insufficient to track predicted future upslope temperature changes (Feeley et al., 2011; Fadrique et al., 2018), lineages within TMFs are only likely to endure through acclimation or adaptation. Narrow elevational ranges (Terborgh, 1977; Lieberman et al., 1996; Perez et al., 2016) and high taxonomic turnover, especially at the cloud-base ecotone (Bach et al., 2007; Baldeck et al., 2016), appear to be the dominant distributional patterns within TMF, yet some lineages, such as the genera *Miconia* (Melastomataceae) and *Meliosma* (Sabiaceae), occupy broad elevational ranges, crossing the cloud-base ecotone. That certain taxa occur across different elevations, spanning ecotones, suggests an ability to tolerate substantial climatic variation. Such lability may be advantageous when responding to climate change. However, it is unclear whether evolutionary heritage further acts as a constraint on which taxa are able to display such broad environmental tolerances and the potential to respond, or adapt, to climate change. Differential evolutionary accessibility to certain adaptations is thought to be common, and frequently phylogenetically clustered (Edwards and Donoghue, 2013). For example, while C4 photosynthesis has evolved multiple times in grasses as a response to decreased CO^2 levels, it is restricted to the PACMAD clade, a lineage possessing a particular set of enabling traits (Christin et al., 2013). Similarly, constraints on adaptation to freezing conditions, combined with niche conservatism, has been proposed as an explanation for the limited number of tropical angiosperm lineages expanding into temperate zones (Wiens and Donoghue, 2004; Mittelbach et al., 2007; Donoghue, 2008; Zanne et al., 2014). If characteristics indicating potential tolerance to climate change, such as the tolerance of broad temperature and moisture regimes associated with wide elevational distribution, are constrained within a few lineages, then the remaining lineages may be considered more vulnerable, with the potential for large losses of phylogenetic diversity within TMF.

Using phylogenetic approaches in order to understand the magnitude to which elevational distribution trends, and the ability to respond to environmental change, are conserved within evolutionary lineages, will contribute to understanding the future of tropical montane forests under a changing climate. The degree of correlation between characteristics, such as elevational distribution, and evolutionary heritage can be quantified by testing for phylogenetic signal (PS), a statistical measure of the non-independence of trait values of taxa due to evolutionary relatedness (Felsenstein, 1985; Losos, 2008; Revell et al., 2008). PS quantifies the tendency for closely related taxa to resemble each other more than they resemble taxa drawn randomly from a phylogeny. Previous studies have found evidence of trait conservatism and phylogenetic signal for diverse characteristics in tropical trees, from mean range size and abundance (Dexter and Chave, 2016) to wood density, size, and mortality rates (Coelho de Souza et al., 2016).

Based on a large Amazon-to-Andes elevation gradient, this study investigates potential evolutionary constraints on elevational distribution and response to environmental change within tropical montane tree lineages. A temporally-calibrated, genus-level phylogeny is generated - covering the breadth of vascular plant diversity, from angiosperms and gymnosperms to pteridophyte tree ferns. Using this phylogeny, we test for evolutionary patterns underlying general elevational distribution trends as well as the influence of the cloud-base ecotone. Specifically, we test two core hypotheses: 1) closely related genera occupy similar elevations, and 2) genera displaying potential for evolutionary lability under environmental change are phylogenetically clustered.

2.3 Methods

2.3.1 Study site

This study is based on a network of 22 1-ha forest inventory plots spread across a 425 to 3625 m asl Amazon-Andes elevation gradient centred on Kosñipata valley, both in and near Manu National Park, south-eastern Peru (Figure 3.1). Established by the An-

des Biodiversity and Ecosystem Research Group (ABERG: www.andesconservation.org), these sites are the subject of ongoing multidisciplinary research (Malhi et al., 2010; van de Weg et al., 2014; Nottingham et al., 2015; Malhi et al., 2017). The gradient encompasses broad variation in habitat and environment, from lowland/submontane forests below 800 m asl, up to the montane forest-puna grassland transition at c.3400 m asl (Girardin et al., 2010). Mean annual temperature decreases from c.24^{o}C at low elevations, to c.9^{o}C at higher elevation (Malhi et al., 2017). Mean total annual precipitation displays a hump shaped trend across the gradient, ranging from c.3000 mm yr^{-1} at low elevations, c.5000 mm yr^{-1} at mid elevations, and c.1000 mm yr^{-1} at high elevations (Rapp and Silman, 2012). Frequent cloud immersion, characteristic of tropical montane cloud forests, occurs above 1500-2000 m asl (Girardin et al., 2010; Rapp and Silman, 2012), reaching peak frequency between 2000-3500 m asl (Halladay et al., 2012). The geological character of the gradient is predominantly Paleozoic meta-sedimentary mudstone with plutonic granite intrusions between 1500-2020 m asl (Nottingham et al., 2018). Soil characteristics change from Haplic Allisols and Haplic Cambisols below 1000 m asl, to Cambisols between 1000-2020 m asl, and Umbrisols above 2520 m asl (Nottingham et al., 2018).

2.3.2 Plot inventory and phylogeny

This study utilises plot inventory data for all living woody stems $>$10 cm diameter at breast height (130 cm above the ground; DBH) growing in 22 plots within the ABERG plot network (Malhi et al., 2010). Plant forms sampled include true trees, tree ferns, palms, and lianas (within 2 m of the ground). Individuals were identified to species-level where possible with field identifications verified through the collection of herbarium specimens and consultation with taxonomic experts. A reference collection is held in the ABERG project herbarium in Cusco, Peru. A total of 289 plant genera were inventoried across all plots. Sequences of the ribulose bisophosphate carboxylase large subunit (rbcL; 267 genera) and maturase-K (matK; 260 genera) plastid genes were obtained from the GenBank database (www.ncbi.nlm.nih.gov/genbank/; Benson et al.

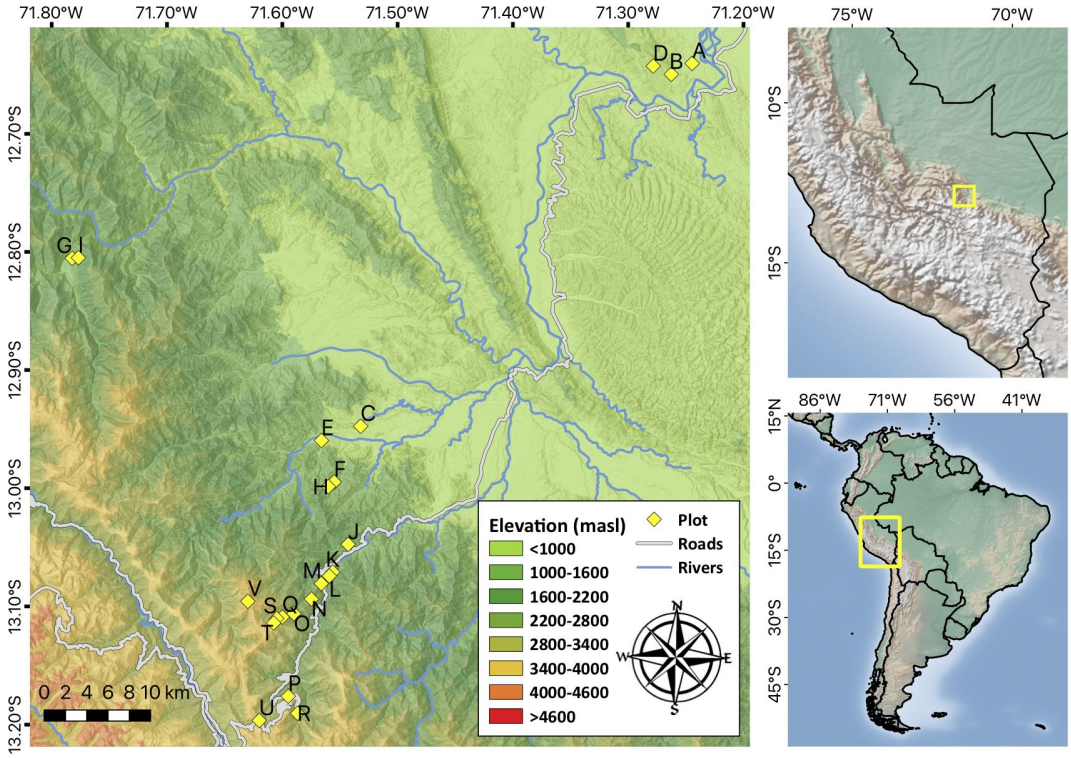

Figure 2.1: Location of 22 plots along an elevation gradient on the Amazonian flank of the south-eastern Peruvian Andes. Yellow diamonds indicate location of plots. Letters relate to the following plots and elevations (m asl): A: PAN-01 (425), B: PAN-02 (595), C: TON-01 (800), D: PAN-03 (850), E: TON-02 (1000), F: SAI-02 (1250), G: CAL-02 (1250), H: SAI-02 (1500), I: CAL-01 (1500), J: SPD-01 (1750), K: TRU-08 (1800), L: TRU-07 (2000), M: TRU-06 (2250), N: TRU-05 (2500), O: TRU-04 (2750), P: ESP-01 (2890), Q: TRU-03 (3000), R: WAY-01 (3000), S: TRU-02 (3250), T: TRU-01 (3450), U: ACJ-01 (3537), V: APK-01 (3625).

2017). Sequences were selected based on geographic proximity to the study gradient, and sequence length. 251 genera have sequences for both rbcL and matK sequences. Sequences were aligned on the MAFFT version 7 online service (https://mafft.cbrc.jp; Katoh et al. 2017). Manual checking of alignment and trimming of sequence ends where data were absent for most genera, was carried out in Mesquite v3.6 (Maddison and Maddison, 2018). As both rbcL and matK are chloroplast markers and the chloroplast does not experience recombination, sequences were concatenated prior to phylogeny estimation.

A maximum likelihood phylogeny was estimated for the 276 genera in RAxML-HPC2 v8.2.10 (Stamatakis, 2015), with rapid bootstrapping (100 iterations), executed on the CIPRES web server (www.phylo.org; Miller et al. 2010) under default settings including a General Time Reversible (GTR) + Gamma (G) model of sequence evolution. Family level relationships within the phylogeny were constrained using the 'R20160415.new' megatree (Gastauer and Meira Neto, 2017), based on the APG IV topology (Chase et al., 2016). Temporal calibration of the phylogeny was conducted utilising penalised likelihood methods in treePL (Smith and O'Meara, 2012) with secondary calibrations on 59 of 275 internal nodes, based on age estimates in Magallón et al. (2015) for angiosperms; Silvestro et al. (2015) for further angiosperms and gymnosperms; Lu et al. (2014) for Podocarpaceae; and Korall and Pryer (2014) for Cyatheaceae.

2.3.3 Elevational distribution trends

In order to test for evolutionary patterns, elevational characteristics of genera were calculated and mapped onto the phylogeny. To quantify similarity of elevational distribution among close relatives, we used abundance weighted mean elevations of genera, based on numbers of individuals per genus within plots. Different approaches were considered to assess the capacity for lineages to respond evolutionarily to novel environmental conditions, including measures of evolutionary lability for mean elevational preference: 1) annual elevational changes in the weighted mean elevation of genera,

with weights based on abundance or relative basal area in plots at different elevations, as quantified for genera on this transect by Feeley et al. (2011) for 38 genera (36 of which are represented in our phylogeny). 2) Elevational range breadth for all 276 genera in the phylogeny, measured as the 95% quantiles of occurrence for each genus on the gradient. 3) Coefficient of variation (CV) for mean elevation of species within a genus, for the 133 genera with more than one species on the transect (the other 143 genera are monotypic across the sampling sites). Both elevational range breadth and CV for mean elevation are indicative of broad environmental tolerances. High values in both measures suggest a genus occupies a breadth of different environmental conditions and may therefore be better able to tolerate climate change. The measures of change in mean elevational position on annual timescales may better represent the potential of genera to respond to ongoing climatic changes (Feeley et al., 2011), but these measures were only available for 36 genera present in our phylogeny. We therefore assessed if our other measures of evolutionary lability (elevational range breadth and CV of mean elevation), which are available for many more genera, are correlated with change measures and may therefore stand in for them.

We estimated phylogenetic signal for elevational characteristics of genera using Pagel's λ (Pagel, 1999; Freckleton et al., 2002). Based on a comparison of tree branch length transformations, λ contrasts variance in observed trait values against expected trait variance under a Brownian motion (BM) model of evolution. Under a BM model, trait values evolve following a stochastic random walk trajectory, with expected trait divergence across each node in the phylogeny being proportional to the phylogenetic depth, or age, of the node. This random walk results in a linear increase in variance with time, and therefore, variance and covariance of trait values between lineages proportional to phylogenetic branch length. Values of λ around 0 indicate no phylogenetic signal. Values of λ around 1 indicate strong phylogenetic signal, matching that expected under a Brownian model of evolution. Values of λ between 0 and 1 indicate intermediate levels of phylogenetic signal. In order to test whether results display metric dependency, we also calculated phylogenetic signal using Blomberg's K (Blomberg

et al., 2003).

2.3.4 The cloud-base ecotone

The influence of the cloud-base ecotone on elevational patterns was analysed by calculating phylogenetic signal for occurrence of genera solely above the cloud-base, below the cloud-base, or across the cloud-base. The elevation of the cloud base is not fixed and varies substantially by location and through time (Foster, 2001). Along our study gradient, the cloud base occurs consistently between approximately 1500-2000 m asl (Girardin et al., 2010; Rapp and Silman, 2012); we used the mid-point of this range (1750 m asl) as the cloud-base elevation in our analysis. To test the robustness of our cloud-base elevation approximation and investigate significant points of taxonomic turnover along the elevation gradient, we additionally used species assemblage information for each plot to conduct a hierarchical cluster analysis, based on Bray-Curtis dissimilarity indices.

Genera were placed into categories based on the distribution of their elevational range. The three categories assigned were 1) only below cloud-base ($\leq$1749 m asl), 2) only above cloud-base ($\geq$1750 m asl), or 3) occurring across the cloud-base (both $<$1749 m asl and $>$1750 m asl). Phylogenetic signal for each distribution category was estimated using the D statistic for binary characters (Fritz and Purvis, 2010). D is based on the sum of sister clade differences. Running opposite to Pagel's λ values, a D value of 1 indicates no phylogenetic signal, and a D value of 0 indicates phylogenetic signal equivalent to that expected under a Brownian model of evolution. Values $<$0 and $>$1 are possible. This observed value is then assessed for significance against the expected sum, generated from simulations (n = 5000) based on an absence of phylogenetic dependency, and phylogenetic structure based on a Brownian model of evolution.

2.4 Results

2.4.1 Elevational distribution trends

Abundance weighted mean elevation shows high and significant phylogenetic signal at the genus level, though slightly less than expected under a Brownian motion model of evolution (λ = 0.79, p$<$0.001). Phylogenetic signal is also observed when gymnosperms and pteridophytes, which occur on long branches, are excluded from the analysis (λ = 0.58, p = $<$0.001). Significant phylogenetic signal here is driven by high and low mean elevation values across a number of lineages (Figure 2.2a). High mean elevation values occur frequently across the Asterids, with the notable exceptions of the Apocynaceae, Rubiaceae, Sapotaceae, and Lecythidaceae which tend towards lower mean elevations. In contrast, low mean elevation values are more dominant within the Rosids; strongly so among the Malpighiales, Fabaceae, and Malvaceae. Exceptional among Rosid lineages, the Oxalidales and Melastomataceae tend towards high mean elevations. Arecaceae, the sole Monocot lineage in the phylogeny displays a low mean elevation pattern. The Magnoliids are largely split between a low mean elevation trend within the Annonaceae and Myristicaceae, and a mid-elevation mean within the Lauraceae. Beyond the angiosperms, the Podocarpaceae and Cyatheales lineages also display largely mid-elevation means. The difference between mean elevations of sister genera pairs (n = 83, mean = 504 m) is 252 m lower than the difference between all genera pairs (n = 37675, mean = 756 m).

The elevational range breadth of genera is positively correlated with annual change in the mean elevation of genera, weighted either by abundance (τ = 0.25, p = 0.03; Figure 2.3a) or relative basal area (τ = 0.48, p $<$ 0.001; Figure 2.3b). The coefficient of variation for mean elevation of species within genera is positively correlated with the elevational change in mean elevation of genera weighted by relative basal area (τ = 0.31, p = 0.007; Figure 2.3d), but not elevational change in mean elevation of genera weighted by abundance (τ = 0.149, p = 0.2; Figure 2.3c). These correlations support our use of elevational range breadth and coefficient of variation for mean elevation as

Figure 2.2: Phylogeny of 276 tree genera with terminal branches coloured according to: **a)** abundance weighted mean elevation; **b)** elevational range size; and **c)** distribution relative to the cloud-base ecotone. There is significant phylogenetic signal for a) mean elevation (λ = 0.79, p $<$ 0.001) and c) distribution solely above (D = 0.50, p $<$ 0.001) or solely below (D = 0.70, p=0.001) the cloud-base ecotone. There is no significant phylogenetic signal for b) genera elevational range size (λ = 0.29, p = 0.23) or c) distribution across the cloud base-ecotone (D = 1, p = 0.48). Major clades are indicated in grey bar to the right side: a = pteridophytes (Cyatheales), b = gymnosperms, c = Magnoliids and *Hedyosmum*, d = Monocots, e = basal Eudicots. Numbered nodes indicate branch stems of lineages mentioned in the main text: 1 = Fabaceae, 2 = Malpighiales, 3 = Oxalidales, 4 = Malvales, 5 = Melastomataceae, 6 = Apocynaceae, 7 = Rubiaceae, 8 = Sapotaceae, 9 = Lecythiadaceae, 10 = Lauraceae, 11 = Annonaceae, 12 = Myristicaceae, 13 = Miconia, 14 = Schefflera, 15 = Meliosma, 16 = Ocotea, 17 = Persea, 18 = Laurales, 19 = Ericales, 20 = Caryophyllales.

proxy measures of the potential ability of species within genera to shift their elevational preference. There is no phylogenetic signal for annual change in the mean elevation of genera, weighted either by abundance (λ = 0.00006, p = 1) or relative basal area (λ = 0.00006, p = 1). Similarly, no significant phylogenetic signal is evident for elevational range size of genera (λ = 0.29, p = 0.23; Figure 2.2b), or the coefficient of variation of species mean elevations within genera (λ = 0.00007, p = 1). Including angiosperm lineages only in the analysis reveals marginally significant values for elevational range size (λ = 0.16, p = 0.04), though this is not consistent across metrics (K = 0.19, p = 0.2).

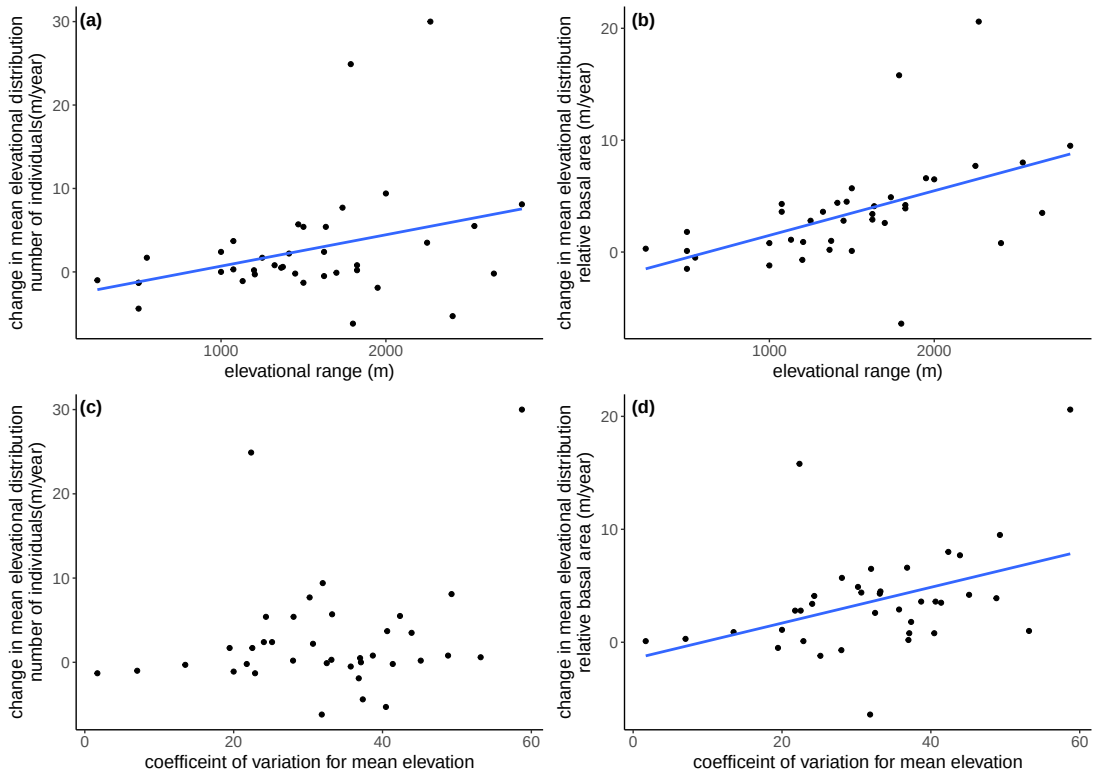

Figure 2.3: The elevational range breadth of genera is positively correlated with annual change in the mean elevation of genera, weighted by: **a)** abundance (τ = 0.25, p = 0.03); and **b)** relative basal area (τ = 0.48, p $<$ 0.001). The coefficient of variation for mean elevation of species within genera is positively correlated with the elevational change in mean elevation of genera weighted by **d)** relative basal area (τ = 0.31, p = 0.007), but not weighted by **c)** abundance (τ = 0.149, p = 0.2). Points represent genera. Correlations based on Kendall's tau coefficient. Blue lines are derived from linear regression.

2.4.2 The cloud-base ecotone

A hierarchical cluster analysis identifies clear dissimilarity in species composition across plots. The greatest turnover in species composition occurs between 1500 and 1750 m asl (Figure 2.4). All plots at 1750 m asl and above are more similar to each other in species composition than they are to all plots at 1500masl and below, and vice-versa. This pattern is driven by the fact that more species reach the limit of their elevational distribution between 1500-1750 m asl than at other elevations, providing support for our use of 1750m both as the approximate elevation for the cloud-base ecotone and as a significant ecological transition zone.

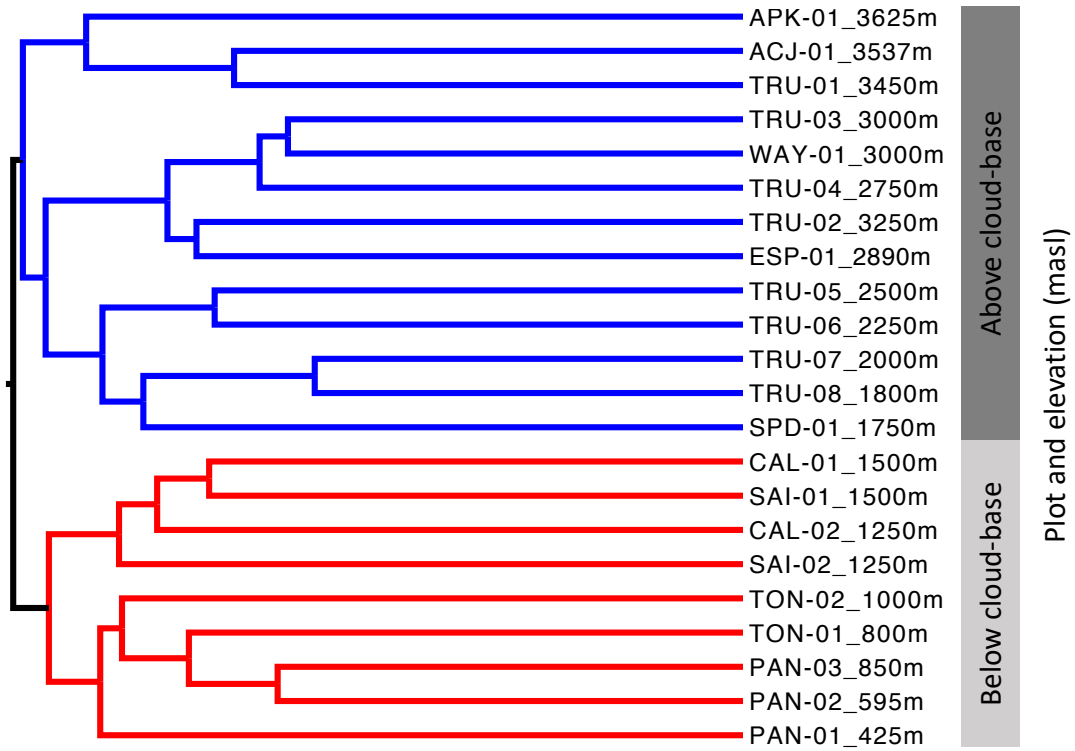

Figure 2.4: Dendrogram generated by a hierarchical cluster analysis based on Bray-Curtis dissimilarity indices, illustrating the main areas of taxonomic turnover across the elevation gradient. Species compositions in all plots at or above 1750 m asl (indicated by blue branches) are more similar to each other than species compositions in all plots at or below 1500m (indicated by red branches) and vice-versa.

Genera distributed solely above the cloud-base ecotone (n = 44) are more significantly clustered in the phylogeny than would be expected under a model of random

phylogenetic structure (D = 0.50, $p < 0.001$; Figure 2.2c). However, the observed phylogenetic signal is significantly less than expected under a Brownian model of evolution ($p = 0.01$). An above cloud-base distribution is more frequent among the Asterids, notably the Asterales, and a clade within the Ericales. Within the Rosids, the Oxalidales are exceptional in a tendency for above cloud-base distribution. The pteridophyte tree ferns also tend towards above cloud-base distributions. Genera occurring at elevations solely below the cloud-base ecotone (n=167) are also more significantly clustered in the phylogeny than expected under a random phylogenetic structure (D = 0.70, p = 0.001; Figure 2.2c), though less than expected under a Brownian model of evolution ($p < 0.001$). Below cloud-base distribution is common among Rosid lineages, notably Fabaceae, Malvaceae, and Malpighiales. There is also a strong trend for below cloud-base distributions within the Apoynanaceae, Sapotaceae, Lecythidaceae, Annonaceae, and Caryophyllales. Those genera occurring across the cloud-base ecotone, i.e. those that show lability in occurrence across this distribution barrier (n=65), are not significantly clustered in the phylogeny (D = 1, p = 0.48; Figure 2.2). These results are also consistent when only angiosperm lineages are considered in analyses.

2.5 Discussion

We find high phylogenetic signal for the mean elevational occurrence of genera, suggesting that evolutionary heritage strongly influences elevational distributions of tree genera within tropical montane forests. The observed phylogenetic signal is higher than that measured previously for a number of tree functional characteristics (Baraloto et al., 2012; Coelho de Souza et al., 2016). Closely related tree genera tend to occupy similar mean elevations, clustering either above or below the cloud-base ecotone and its associated environmental barriers. Further, those genera that occur above the cloud base show stronger phylogenetic clustering than those below the cloud base. While the general pattern is for narrow elevational ranges of genera as a whole, some genera appear able to escape this evolutionary constraint, occupying large elevational ranges and crossing the cloud-base ecotone. These more broadly distributed gen-

era are not phylogenetically clustered, but rather seem to arise randomly across the breadth of vascular plant lineages represented in our phylogeny.

That closely related genera tend to occupy similar mean elevations is evidence for the influence of evolutionary heritage on biodiversity distribution across the heterogeneous environment of tropical montane forests. This observed trend, in combination with high taxonomic turnover (Malhi et al., 2010; Jankowski et al., 2013; Baldeck et al., 2016) and narrow elevational ranges (Perez et al., 2016), is consistent with the prediction of niche conservatism that it tends to be hard for lineages to evolve environmental tolerances that differ markedly from those of evolutionary ancestors (Donoghue, 2008; Wiens et al., 2010). The phylogenetic clustering of closely related genera solely above, and solely below, the cloud-base ecotone reinforces this pattern. Associated with sharp climatic changes, such as reduced solar radiation and increased occult precipitation, the cloud-base ecotone may represent an important environmental barrier, constraining the movement of lineages between contrasting environments or elevational thresholds (Fadrique et al., 2018). A hierarchical cluster analysis revealing strong dissimilarity in species composition between plots above versus below the cloud-base, provides further evidence for the significance of this ecotone as an area of ecological transition (Figure 2.4). Higher phylogenetic signal for lineages distributed solely above the cloud-base ecotone compared to those solely below suggests that clustering of lineages, evolutionary conservatism, and potential environmental filtering, is stronger within tropical montane cloud forest. TMCF and the conditions associated with frequent cloud immersion may represent an ecologically harsh environment, possessing a unique evolutionary diversity which is constrained above the cloud-base ecotone.

It is important to note that while the characteristics analysed show significant phylogenetic signal, this signal is less than that expected under a Brownian motion (BM) model of evolution, where λ values would be close to 1 and D values close to 0. This may be the result of divergent selection amongst closely related taxa and/or convergent evolution across distant relatives. On the other hand, a simple BM model may not accurately describe genus-level distribution changes over time. For example, a

simple BM model does not account for variation in rates of evolution over time or among lineages. Different models of evolution are possible, however since our goal was simply to identify the existence of phylogenetic signal and not to test any specific underlying mechanism, a BM model can provide insight into elevational patterns of high taxonomic turnover and constraint to narrow elevational distributions and particular habitats.

Most genera evidently occupy relatively narrow elevational distributions. However, a few genera, such as *Miconia* (Melastomataceae), *Meliosma* (Sabiaceae), *Ocotea* (Lauraceae), *Persea* (Lauraceae) and *Schefflera* (Araliaceae), seem able to escape the constraints of evolutionary heritage and occupy large elevational ranges, as well as cross the ecotonal transitions at the cloud-base (Figure 2.2b-c). In addition to occupying broad elevational ranges, genera such as *Miconia*, *Persea*, and *Schefflera*, are among those that show significantly greater upslope shifts in mean elevation than tree genera as a whole (Feeley et al., 2011). In the cases of *Miconia* and *Schefflera*, rates of elevational change have actually kept pace with predicted temperature increases, which contrasts with most other tree genera that are lagging in their responses to temperature increases (Malhi et al., 2009; Urrutia and Vuille, 2009; Feeley et al., 2011). Such trends in specific genera, along with the more general correlation observed between elevational range size and rate of elevational distribution change (Figure 2.3a-b), reinforce the suggestion that occupancy of a broad elevational range may be associated with a greater lability of response to the pressures of a changing climate. In any case, our findings reveal no phylogenetic signal for elevational range size (Figure 2.2b) or annual rate of elevational distribution change, demonstrating that characteristics such as broad elevational ranges, or trends of upslope distribution change, are not phylogenetically clustered among closely related genera. Rather, such genera come from lineages distributed across the breadth of the vascular plant phylogeny.

The observed random phylogenetic pattern for elevational range size provides an interesting contrast to research revealing clear phylogenetic signal for geographic range size across Amazonian tree lineages (Dexter and Chave, 2016). However, the

environmental drivers of elevational range sizes, more closely linked to abiotic tolerances (Janzen, 1967; Ghalambor et al., 2006), are likely to be different to those operating on range size in the tropical lowlands. While phylogenetic signal is not evident for elevational range size across the breadth of vascular plant genera considered in this analysis, there appears to be a trend for broad elevation ranges in a few lineages, notably the Laurales (Figure 2.2b). Such lineages may drive the marginally significant phylogenetic signal observed for elevational range size when only angiosperms are included in the analysis.

Although lability of response to environmental change, indicated by occupancy of a broad elevational range, or upslope change in elevation distribution, is not clearly constrained within certain evolutionary lineages, the majority of lineages nonetheless occupy narrow elevational ranges, and the timescale necessary for evolutionary adaptation within most tree lineages may be incompatible with the current rapid rate of environmental change (Bush et al., 2004; Feeley et al., 2011; Pepin and Mountain Research Initiative EDW Working Group, 2015). Clustering of closely related genera around similar mean elevations may suggest that climatic trends, such as rising temperatures, will have unequal impacts across lineages. Lowland lineages, already occupying broad distributions across the Amazon, may find that amenable environmental conditions become available on higher ground. Meanwhile those few lineages already occupying broad elevational distributions may find themselves at a competitive advantage in terms of tolerating changing conditions. However, TMF lineages, and the evolutionary diversity constrained to mid and high elevations may be at risk. As climate conditions track up mountain slopes, the area of land amenable to TMF lineages will be reduced in size or disappear completely. At the same time TMF lineages may be squeezed from below by increasing competition as lowland lineages migrate upslope (Colwell et al., 2008; Feeley et al., 2011). Among TMF lineages, those clustered solely above the cloud-base ecotone may be most vulnerable. Many TMCF tree lineages display unique adaptation to the conditions associated with frequent cloud immersion, such as high foliar water uptake, which make them highly specialised and

at risk under a changing climate (Eller et al., 2016). With lineages constrained by evolutionary heritage to narrow elevational distributions and particular habitat, climatic changes such as a decline in frequency of cloud immersion and lifting of the cloud base (Still et al., 1999; Helmer et al., 2019), may fundamentally alter the tropical montane environment and result in large population reductions and potential extinctions among the TMF biota. Phylogenetic clustering in the elevational distribution of TMF tree lineages means any extinctions may lead to a disproportionate loss of evolutionary history, a risk which is particularly stark for specialised lineages constrained to TMCF.

A degree of perspective must be given to interpretation of phylogenetic analyses at the genus-level. Some genera contain many species and may represent great variation in ecological and functional characteristics. However, focusing on higher taxonomic levels, such as genera, can be a valuable means to understanding deeper evolutionary trends. While species-level analyses may reveal patterns at a finer scale, DNA sequence data is simply not yet available for an analysis representing the phylogenetic breadth we are able to consider at the genus level. In addition, most species in this data set are only recorded in a single plot and therefore, given the elevational interval between plots, quantification of their elevational distribution would have limited accuracy. A genus level analysis is also advantageous in that it minimises potential errors created by any individuals not reliably identified to species. Nevertheless, future analyses of lineage specific species level phylogenetic trends across elevation, particularly focusing on functional characteristics, would further develop our understanding of the mechanisms driving elevational distribution patterns.

Overall, our study illustrates that by utilising phylogenetic approaches we can better understand how evolutionary heritage, and the tendency of close relatives to share similar ecological and functional characteristics, influences lineage distribution patterns across different environments. In particular, our analyses draw out the ecological significance of environmental transition zones, such as the cloud-base ecotone. Further, by demonstrating clustering of evolutionary lineages at similar elevations, we

provide valuable insight into the potential impact rapid environmental changes may have on the unique and vulnerable evolutionary diversity of tropical montane forests in general, and tropical montane cloud forests in particular.

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Chapter 3

Trends in taxonomic and phylogenetic richness along a tropical montane forest elevation gradient

3.1 Abstract

Consensus around the nature of the elevational diversity gradient is lacking, with much variation in observed patterns dependent on the dimension of diversity considered. We investigate taxonomic and phylogenetic richness patterns in tree lineages across a tropical montane forest elevation gradient from 425 to 3625 m asl. We reveal non-linear elevational trends in all richness metrics considered. Most notably, evolutionary diversity is highest at mid-elevations $\sim$1500 m asl. This trend in evolutionary diversity is driven by elevational variation in the evolutionary age structure of communities. Elevational distribution trends vary between younger and older evolutionary lineages. For example, 53% of lineages that are 10 million years old occur only below 1750 m asl, while just 13% of lineages that are 110 million years old occur only below 1750 m asl. Our results do not support predictions of the Tropical Niche Conservatism and Out of the Tropics hypotheses for a montane flora that is simply a less diverse, younger subset of the lowland flora. Rather, we show that the tree lineage richness of mid-elevation tropical montane forest may rival that of the Amazonian lowlands, especially when factoring in variation across evolutionary depths.

3.2 Introduction

Understanding spatial variation in biodiversity is a fundamental goal of ecology. Gradients of environmental factors, such as temperature and precipitation, have long been thought to shape patterns of diversity (Humboldt and Bonpland, 1805; Schimper, 1903; Rosenzweig, 1995), while the frequently non-linear nature of such ecological trends is increasingly recognised (D'Amario et al., 2019). The elevational diversity gradient is a widely observed ecological pattern, yet its ubiquity and uniformity, along with its underlying mechanisms, remain without consensus (Rahbek, 1995; Guo et al., 2013). Further, linearly changing environmental gradients are not fully established as the main drivers of variation in the spatial organisation of biodiversity. Environmental thresholds or barriers, such as freezing conditions (Zanne et al., 2014), may be more important

in shaping observed patterns. In addition to ecological factors, evolutionary processes such as niche conservatism, can also act on diversity distributions across different environments (Wiens and Donoghue, 2004; Wiens et al., 2010). Here we investigate tree diversity along a tropical montane elevation gradient. Specifically, we compare both taxonomic and phylogenetic richness patterns, and further explore the evolutionary dimension of elevational diversity trends.

One of the most iconic, large-scale diversity patterns within ecology is the latitudinal diversity gradient (LDG), the long-established observation of decreasing diversity from the tropics towards the poles (Pianka, 1966; Mittelbach et al., 2007). Though documented perhaps more frequently than any other diversity trend, agreement on the causes of this latitudinal pattern is lacking. Relationships between diversity and multiple environmental variables, such as temperature and precipitation (Currie, 1991; Currie et al., 2004; Kreft and Jetz, 2007) have been put forth to explain the LDG. Meanwhile, evolutionary and biogeographic mechanisms have also been proposed (Mittelbach et al., 2007), such as hypotheses based on niche conservatism (Wiens and Donoghue, 2004), or diversification rate variation (Rosenzweig, 1995).

While less prominent than the LDG, the elevational diversity gradient (EDG) is a widely accepted ecological trend. Rahbek (1995) traced a generalised belief in the monotonic decrease in taxonomic richness with elevation back to a handful of studies, including Terborgh's notable work on birds in the Peruvian Andes (Terborgh, 1977). However, great variation is documented in the shape of the elevational diversity gradient, both across taxa and regions. Linear and hump-shaped patterns of richness with elevation, as well as invariance of richness with elevation until some threshold elevation is reached, above which diversity declines, are all frequently observed (Rahbek, 1995; Lomolino, 2001; Guo et al., 2013). Similarly, the generality of a diversity trend specific to trees along tropical montane elevation gradients is unclear. Linear decreases above 1500 m asl (Gentry, 1988; Vazquez and Givnish, 1998; Jankowski et al., 2013), hump-shaped patterns (Kessler, 2000; Girardin et al., 2014), and indeed no elevational trend in richness (Tiede et al., 2015), have all been reported. The

shape of the EDG provides important context to any consideration of the biodiversity of montane ecosystems.

Historically, the study of diversity gradients has focused on taxonomic richness and environmental drivers, such as temperature. Yet phylogenetic richness and evolutionary processes may also modulate diversity trends. The development of modern phylogenetic approaches (eg. Faith 1992; Webb et al. 2002) allows evolutionary patterns and processes to be factored into analyses concerning the spatial variation in biodiversity. One prominent evolutionary perspective suggests that a key driver of global patterns of biodiversity is phylogenetic niche conservatism, the tendency towards retention of ancestral characteristics (Wiens and Donoghue, 2004). For example, species tend to be found in environments similar to those inhabited by their ancestors (Wiens and Donoghue, 2004; Holt, 2009). This suggestion has been logically expanded upon in the Tropical Niche Conservatism (TNC) and the Out of the Tropics (OTT) hypotheses (Wiens and Donoghue, 2004; Jablonski et al., 2006). Making the assumption that most lineages evolved in a tropical environment (Davies et al., 2004; Ruddiman, 2007), and that species tend to retain the physiological tolerances of their ancestors (Wiens and Donoghue, 2004; Holt, 2009), the TNC and OTT hypotheses predict that species richness, evolutionary diversity, and lineage age will be highest in present day tropical climates. Migrations to colder, temperate environments are thought to be infrequent or recent (Wiens and Donoghue, 2004), and as such, temperate regions are predicted to hold less richness, lower evolutionary diversity, and younger lineages, essentially comprising a depauperate subset of the lowland tropical biota (Wiens and Donoghue, 2004; Hawkins et al., 2011; Kerkhoff et al., 2014). These predictions can be, and have been, extended to tropical elevation gradients (Segovia and Armesto, 2015; Qian, 2017). Decreasing temperature with increasing elevation (Schimper, 1903; Körner, 2007), along with changes in precipitation (Rapp and Silman, 2012) and solar radiation (Fyllas et al., 2017), result in environmental conditions becoming distant from the wet and warm lowland tropical 'optimum'. As such, diversity and evolutionary age might be expected to decrease with elevation.

Current evidence for TNC and OTT as drivers of large-scale diversity patterns is mixed. In support, angiosperm family mean age is reported to decrease away from the equator (Hawkins et al., 2011; Romdal et al., 2013), and latitudinal bands decrease in evolutionary diversity towards the poles (Kerkhoff et al., 2014). However, contrary to predictions of TNC and OTT for the LDG, temperate forests contain a diverse and evolutionarily distinct flora, derived from extra-tropical elements, rather than a younger, less diverse subset of the tropical flora (Qian et al., 2014; Segovia and Armesto, 2015). Additionally, biome affiliation and climate, rather than latitude per se, may be the key spatial determinants of evolutionary diversity for woody plants (Rezende et al., 2017). Across elevation gradients, evolutionary diversity and family age have been found to increase with elevation (Segovia and Armesto, 2015; Tiede et al., 2015), diverging from the expectations of TNC and OTT. It is worth noting that many studies around TNC and OTT utilise taxonomically derived family ages. Given taxonomists may circumscribe families differently across lineages, mean family age may not provide the most consistent estimation of evolutionary age among floras. In any case, the lack of consensus regarding TNC and OTT suggest further studies are required, and the elevational diversity gradient within tropical montane forest (TMF) provides a compelling test case.

The tendency for temperature regimes to become more ecologically restrictive with increased elevation (Nagy and Grabherr, 2009) has led some to consider the EDG to be intuitively similar to the LDG (Stevens, 1992). In reality, the environmental changes that occur across elevation may be distinct from those that occur across latitude. For example, along elevation gradients, there is often a relatively stable condensation zone where clouds tend to form (Jarvis and Mulligan, 2011). This cloud zone is particularly prominent in the tropics and does not exist along latitudinal gradients. Further, it has been suggested that environmental thresholds, such as freezing temperatures (Zanne et al., 2014), or eco-geographic barriers, such as the subtropical arid belt (Smith et al., 2012; Bacon et al., 2013), rather than environmental gradients per se underpin broad patterns in biodiversity distribution. The mid-elevation transition at the cloud-base

ecotone (into tropical montane cloud forest; TMCF) may form a key environmental threshold, or barrier. The cloud-base ecotone is associated with substantial shifts in key environmental factors, for example precipitation (Rapp and Silman, 2012) and soil properties (Whitaker et al., 2014; Nottingham et al., 2015). These environmental step changes may present an ecological barrier for some tree lineages (Bruijnzeel, 2001; Fadrique et al., 2018). For instance, solar radiation, which decreases under cloud immersion, and becomes diffuse (Fyllas et al., 2017), has been suggested as a key influence on plant distribution patterns (Jaramillo and Cárdenas, 2013).

TMF of the Tropical Andes, and TMCF within them, are a biodiversity hotspot and centre for endemism of global importance (Myers et al., 2000). In addition to this conservation importance, TMF provide vital ecosystem functions, influencing carbon and nutrient cycling (Girardin et al., 2010; Spracklen and Righelato, 2014; van de Weg et al., 2014), and regulating hydrological processes (Bruijnzeel et al., 2011). Yet these unique habitats are vulnerable. Experiencing changes to precipitation regimes (Hu and Riveros-Iregui, 2016), and rapidly rising temperatures (Pepin and Mountain Research Initiative EDW Working Group, 2015; Russell et al., 2017), there is a high risk of substantial diversity loss within TMF under ongoing environmental change (Feeley and Silman, 2010a,b). As such it is imperative to identify general elevational diversity patterns, as well as areas representing high levels of both taxonomic and evolutionary diversity.

Tropical montane forests, encompassing a considerable climatic range, provide a natural testing ground for hypotheses which attempt to explain large-scale patterns of biodiversity distribution. Here we consider the Tropical Niche Conservatism and Out of the Tropics hypotheses, testing the predictions that evolutionary diversity and evolutionary age of taxa decrease with increased elevation. More specifically, clarifying the elevational richness patterns of tree lineages within TMF will add depth to our understanding of this unique ecosystem. In this analysis we address three core questions: 1) What is the shape of the elevational richness gradient within tropical montane forest? 2) Do elevational trends of taxonomic and phylogenetic richness differ? 3) Is

there elevational variation in the evolutionary age structure of communities?

3.3 Methods

3.3.1 Study site and plot inventory

We utilise plot census data for all woody stems >10 cm diameter at breast height (130 cm above the ground; DBH) from a network of 23 one hectare forest plots located along an Amazon-to-Andes elevation gradient from 425-3625 m asl. Established and maintained by the Andes Biodiversity and Ecosystem Research Group (ABERG: www.andesconservation.org), the plot network is centred on the Kosñipata valley, within and on the edge of Manu National Park, south-eastern Peru (Figure 3.1). From lowland/sub-montane forests at 425 m asl, up to the tropical montane forest-puna grassland transition at c.3400 m asl (Girardin et al., 2010), the gradient encompasses large variation in habitat and environmental variables. Around 1500-2000 m asl the cloud-base ecotone marks the start of tropical montane cloud forest (Girardin et al., 2010; Rapp and Silman, 2012), with a characteristic cloud immersion which reaches peak frequency between 2000-3500 m asl (Halladay et al., 2012). Across the gradient mean annual temperatures range from c.24^{o}C at low elevations, to c.9^{o}C at higher elevation (Malhi et al., 2017). Mean total annual precipitation follows a non-linear trend from c.3000 mm yr^{-1} at low elevations to c.5000 mm yr^{-1} at around 1000m, then declining monotonically to c.1000 mm yr^{-1} at highest elevations (Rapp and Silman, 2012).

3.3.2 Phylogeny

Across all plots, a total of 301 plant genera were identified. Sequences for the plastid genes rbcL and matK were collated from the GenBank database (www.ncbi.nlm.nih.gov/genbank/; Benson et al. 2017), for 266 and 259 of these genera respectively (250 genera represented by both rbcL and matK sequences). Sequence alignment was conducted using the MAFFT version 7 online service (https://mafft.cbrc.jp; Katoh et al. 2017), with manual checking and trimming of sequence 'ragged ends' carried out in

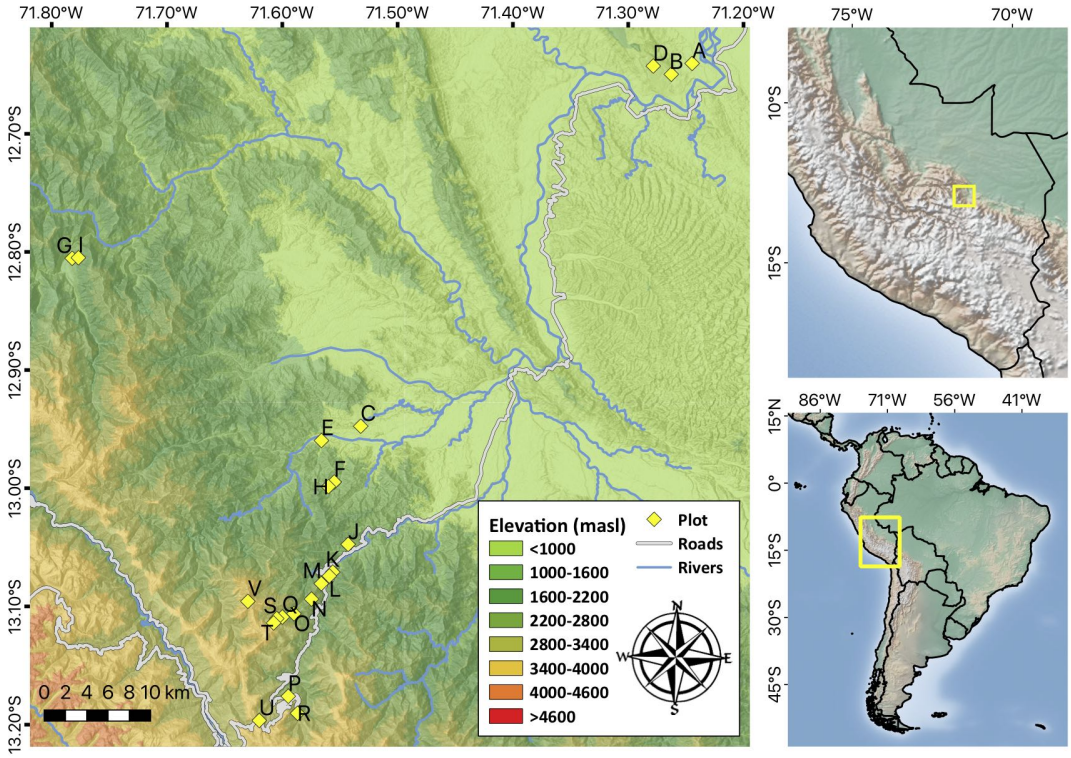

Figure 3.1: Location of 23 plots along an elevation gradient on the Amazonian flank of the south-eastern Peruvian Andes. Yellow diamonds indicate location of plots. Letters relate to the following plots and elevations (m asl): A: PAN-01 (425), B: PAN-02 (595), C: TON-01 (800), D: PAN-03 (850), E: TON-02 (1000), F: SAI-02 (1250), G: CAL-02 (1250), H: SAI-02 (1500), I: CAL-01 (1500), J: SPD-01 (1750), K: TRU-08 (1800), L: TRU-07 (2000), M: TRU-06 (2250), N: TRU-05 (2500), O: TRU-04 (2750), P: ESP-01 (2890), Q: TRU-03 (3000), R: WAY-01 (3000), S: TRU-02 (3250), T: TRU-01 (3450), U: ACJ-01 (3537), V: APK-01 (3625).

Mesquite v3.6 (Maddison and Maddison, 2018). As chloroplast markers, neither rbcL or matK experience recombination. Therefore, sequences were concatenated prior to phylogeny estimation.

For the 275 genera with sequence information we estimated a maximum likelihood phylogeny in RAxML-HPC2 v8.2.10 (Stamatakis, 2015), executed on the CIPRES web server (www.phylo.org; Miller et al. 2010) under default settings, including a General Time Reversible (GTR) + Gamma (G) model of sequence evolution. We constrained family level relationships within the phylogeny using a published angiosperm family tree (Gastauer and Meira Neto, 2017), which follows the APG IV topology (Chase et al., 2016). We carried out temporal calibration of the phylogeny using a penalised likelihood method in treePL (Smith and O'Meara, 2012) with secondary calibrations on 59 of 275 internal nodes, based on age estimates in Magallón et al. (2015) for angiosperms, Silvestro et al. (2015) for gymnosperms and further angiosperms, Lu et al. (2014) for Podocarpaceae, and Korall and Pryer (2014) for Cyatheaceae.

3.3.3 Taxonomic and phylogenetic richness

Given numerous indeterminate and morpho-species identifications, we quantified the taxonomic richness of plots as the number of genera. Genus richness also provides equivalence with phylogenetic metrics, necessarily based on the genus-level phylogeny. We used multiple metrics to quantify different aspects of phylogenetic richness for each plot. Faith's phylogenetic diversity (PD) is calculated as the sum of all the branch lengths of a phylogeny for taxa in a community, including the root stem (Faith, 1992) and is weighted toward diversity in recent evolutionary time (Dexter et al., 2019). We also calculated the standard effect size of phylogenetic diversity (sesPD), which is obtained by comparing the observed phylogenetic diversity versus expected phylogenetic diversity. Expected diversity is estimated by random shuffling of the phylogeny tips. Positive values of sesPD indicate greater diversity than expected, negative values indicate less diversity than expected. Lastly, we calculated the time-integrated lineage diversity (TILD) which evenly weights phylogenetic diversity across recent and deep

evolutionary time and is calculated by integrating the area under a lineage through time plot (sensu Yguel et al. 2016), after log-transforming the y-axis, or the number of lineages at each time point (Dexter et al., 2019). PD and sesPD were calculated using the 'picante' package (Kembel et al., 2010), TILD was calculated using a new function published in Dexter et al. (2019).

Richness is influenced by sample size (Colwell et al., 2012), and there is large variation in the number of individual stems sampled across plots (min = 459, max = 1516). Therefore we rarefied plot data before calculation of richness metrics. For taxonomic richness we rarefied samples to 459 individual stems per plot, since this was the lowest number recorded across plots. Since calculation of phylogenetic metrics is necessarily based only on genera included in the phylogeny, plot samples were first subset to these lineages and then rarefied to 320 individual stems per plot (equal to the lowest number of individual stems recorded in a plot that belonged to genera present in the phylogeny). We conducted 100 rarefactions and from these calculated the mean of each metric for each plot. Rarefactions were conducted using the 'rrarefy' function in the 'vegan' package (Oksanen et al., 2018). We then conducted pairwise correlations of the metrics, based on Spearman's rank correlation coefficient.

We applied linear, quadratic, and breakpoint regression models in order to identify which pattern best describes the elevational richness gradient for each metric. Linear and quadratic regression were conducted using the 'lm' function in the R package stats (Team, 2018). Breakpoint regressions were conducted using the 'segmented' function in the R package segmented (Muggeo, 2008). The model with best fit was established based on a comparison of R^2 values. Due to the potentially strong influence of the long branch lengths leading to tree ferns and gymnosperm, all analyses were repeated excluding these lineages and considering only angiosperms.

3.3.4 Evolutionary age structure

We further investigated the evolutionary dimension of diversity patterns by considering the elevational distribution trends of lineages at different evolutionary depths. We calculated the number of lineages along with their elevational range at evolutionary depth intervals of every 10 million years across the full 382 million-year evolutionary span of our phylogeny (our age estimate for the split between seed plants and ferns). We additionally calculated which elevations are occupied by the highest number of lineages at each 10 million year interval of evolutionary depth. As an illustration, at an evolutionary depth of 200 million years, there are a total of three lineages in our phylogeny (Figure 3.4 and Figure 3.5a). One branch leading to all angiosperms, one branch leading to all gymnosperms, and one branch leading to all tree ferns. In terms of elevational range, angiosperms occur from 425-3625 m asl, gymnosperms occur from 1250-3000 m asl, and tree ferns occur from 800-3450 m asl. Thus, the maximum lineage diversity at an evolutionary depth of 200 million years is found between 1250-3000 m asl, where all three lineages are present, while outside this range there are only one or two lineages of this evolutionary depth.

3.4 Results

3.4.1 Taxonomic and phylogenetic richness

Across all 23 plots, but excluding individuals (n = 458) not identified to genus, a total of 20,926 individuals were recorded, belonging to 301 genera and 100 families. The most abundant genera were *Cyathea* (2410 individuals), *Weinmannia* (1843 individuals), and *Miconia* (1530 individuals). Based on the raw data, the highest generic richness occurs in plot SPD-02 at 1500 m asl, with a total of 109 genera. After rarefaction, accounting for the effect of variation in stem density, the highest generic richness remains in plot SPD-02, at 1500 m asl, with a mean of 88 genera per 459 individuals (Figure 3.2a). After rarefaction, the highest mean values for phylogenetic richness metrics occur at 1500 m asl for PD (plot SPD-02 = 6198 (myrs); Figure 3.2b), 3450

m asl for sesPD (plot TRU-01 = $+2.17$; Figure 3.2c), and 1500 m asl for TILD (plot SAI-01 = 664 (log(myrs)); Figure 3.2d).

Pairwise correlations show that, with the exception of sesPD with TILD, all metrics display significant positive or negative correlations with each other (Figure 3.3). Genus richness has a significant positive correlation with PD (rho = 0.91, p $<$0.001), a weak positive correlation with TILD (rho = 0.51, p $<$0.05), and a negative correlation with sesPD (rho = -0.79, p $<$0.001). PD is negatively correlated with sesPD (rho = -0.66, p $<$0.001), and positively correlated with TILD (rho = 0.74, p $<$0.001). sesPD and TILD are not correlated (rho = -0.15, p $>$0.05). Despite these pairwise correlations, the elevational patterns found across the different richness metrics differ in terms of model fit (Table 3.1). The elevational pattern of genus richness is best described by a breakpoint regression (R^2 = 0.89), though this fit is not markedly better than for linear (R^2 = 0.87) or quadratic regressions (R^2 = 0.87). The genus richness of plots is relatively constant up until an estimated breakpoint at 1376 m asl ($\pm$329m), above which genus richness decreases with elevation (Figure 3.2a). A break point regression also provides the best fit for the elevational pattern of PD (R^2 = 0.93), which increases in value up to an estimated breakpoint at 1401 m asl ($\pm$131m), and then decreases with further elevation (Figure 3.2b). The pattern of sesPD across elevation (Figure 3.2c) is best described by a quadratic regression model (R^2 = 0.83). TILD follows a hump-shaped pattern across elevation (Figure 3.2d), with a quadratic regression giving the best fit to the data (R^2 = 0.76).

Table 3.1: Comparison of regression model fits for elevational patterns of genus richness, phylogenetic diversity (PD), standardised effect size phylogenetic diversity (sesPD), and time-integrated lineage diversity (TILD). Numbers in bold indicate highest model R^2 value for each diversity measure.

	Linear regression		**Quadratic regression**		**Breakpoint regression**	
	R^2	**p-value**	**R^2**	**p-value**	**R^2**	**p-value**
Genus richness	0.87	$<$0.001	0.87	$<$0.001	**0.89**	na
PD	0.81	$<$0.001	0.88	$<$0.001	**0.93**	na
sesPD	0.67	$<$0.001	**0.82**	$<$0.001	0.81	na
TILD	0.19	0.023	**0.76**	$<$0.001	0.65	na

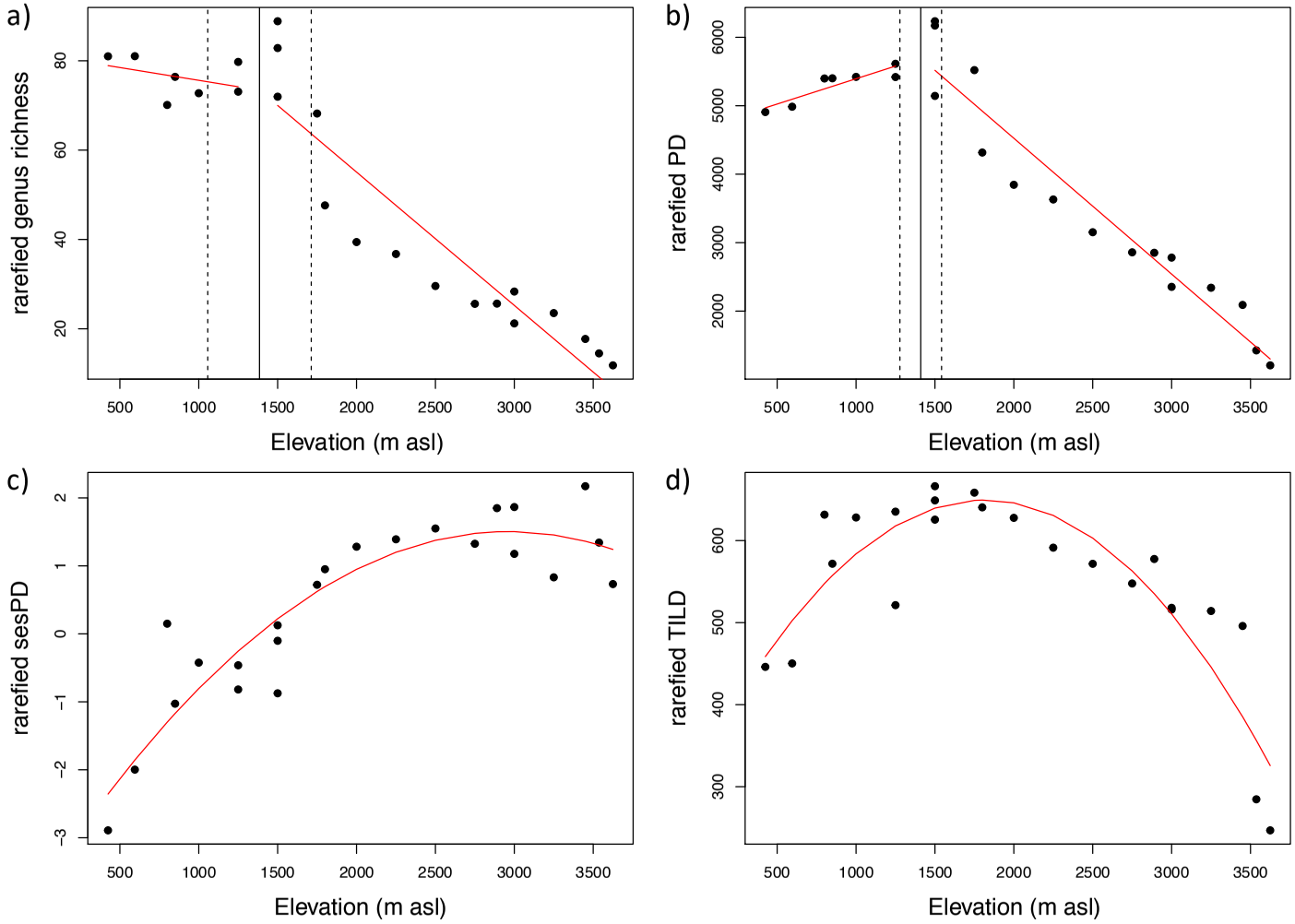

Figure 3.2: The shape of the elevational richness gradient varies between metrics. **a)** Genus richness and **b)** phylogenetic diversity (PD) are best described by breakpoint regression models, while **c)** standardised effect size phylogenetic diversity (sesPD) and **d)** time integrated lineage diversity (TILD) are best described by quadratic regression models. Points are mean rarefied metric values for each plot. Red lines represent regression lines from the best fitting model for each metric. For figures a and b, the solid vertical line indicates the estimated breakpoint, with respective standard error represented by vertical dashed lines.

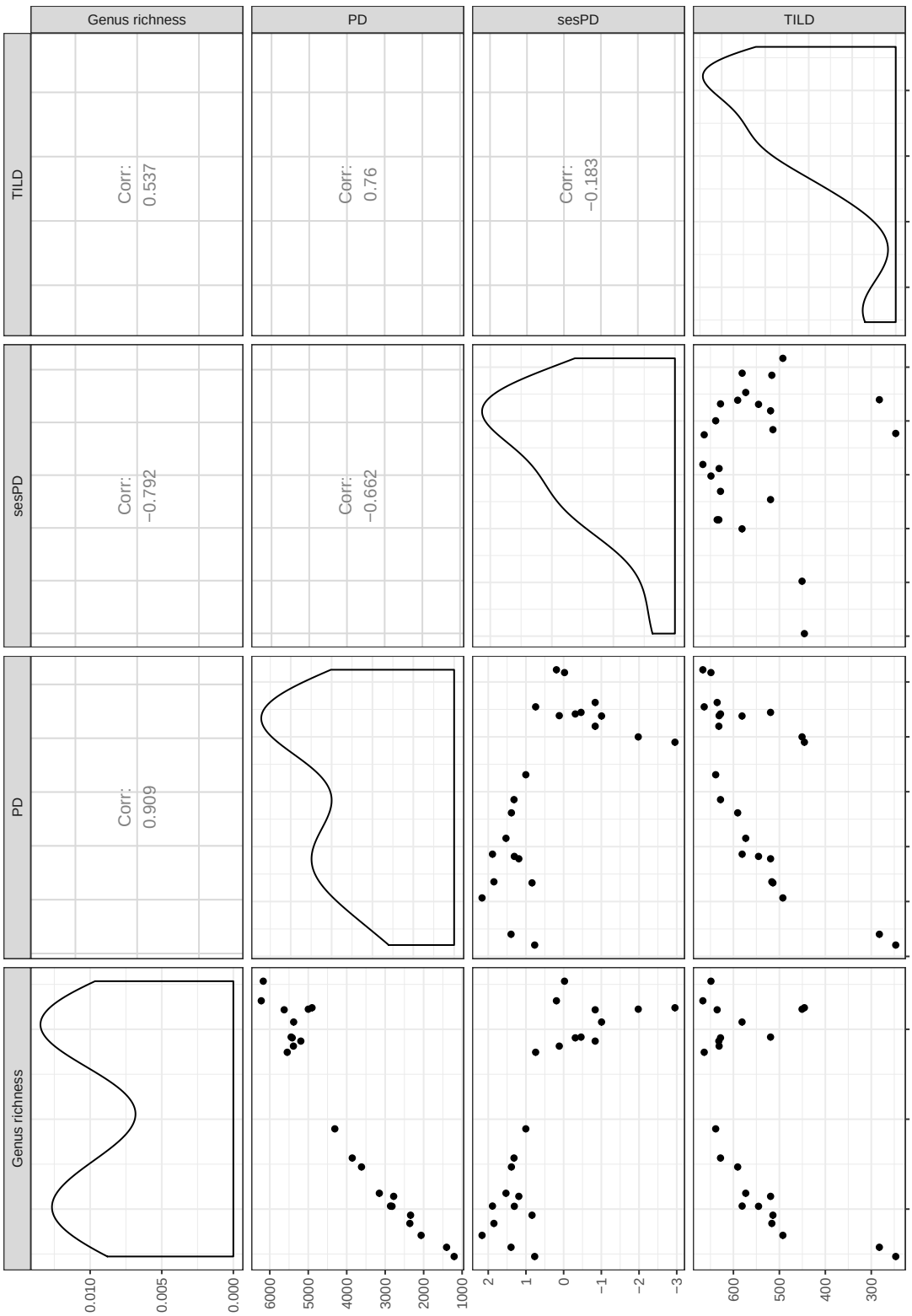

Figure 3.3: Pairwise correlations between taxonomic and phylogenetic measures of the elevational diversity gradient within tropical montane forest. Correlations based on Spearman's rank correlation coefficient.

3.4.2 Evolutionary age structure

Only extant lineages are included in our phylogeny. Therefore, the number of lineages at different evolutionary depths necessarily increases from 2 lineages at 382 million years old (1 lineage leading to tree ferns, 1 lineage leading to seed plants), to 275 present day lineages, equal to the total number of genera in plots that are present in our phylogeny (Figure 3.4). The pattern of elevational range distribution of lineages varies at different evolutionary depths. Six notable evolutionary depths are presented in Table 3.2 and Figure 3.5a-f.

Table 3.2: Summary of lineage elevational range trends and richness at six notable evolutionary depths.

Evolutionary depth (myrs)	Total no. lineages	No. lineages only $<$1750 m asl	No. lineages only $>$1750 m asl	Elevations of peak lineage richness (m asl)	No. lineages at richness peak
10	238	125	17	1300-1500	117
70	101	33	9	1300-1500	65
110	30	4	1	1300-1500	27
120	16	1	1	1300-1900	13
130	8	0	1	1500-2000	7
200	3	0	0	1300-3000	3

At an evolutionary depth of 10 myrs (Figure 3.5f), there are 238 lineages that presently occur along the elevation transect. 125 of those lineages do not presently occur above 1750 m asl, which could be due to a lowland tropical origin and failure to adapt to environmental conditions at higher elevations. There are also 17 lineages at 10 myrs evolutionary depth that only occur above 1750 m asl, which could mean that they have been occupying high elevation environments for at least 10 myrs and have not managed to colonise the lowlands. The peak in the number of 10 myr old lineages (n = 117) is between 1300-1500 m asl (Figure 3.5g). At an evolutionary depth of 70 myrs (Figure 3.5e), there are 101 lineages that presently occur along the elevation transect. 33 of those lineages do not presently occur above 1750 m asl and 9 lineages do not occur below 1750 m asl. The peak in the number of 70 myr old lineages (n = 65) is between 1300 and 1500 m asl (Figure 3.5g). At an evolutionary depth of 110 myrs (Figure 3.5d), there are 30 lineages that presently occur along the elevation transect. 4 of those lineages do not presently occur above 1750 m asl and 1 does not occur below 1750 m asl. The peak in the number of 110 myr old lineages (n

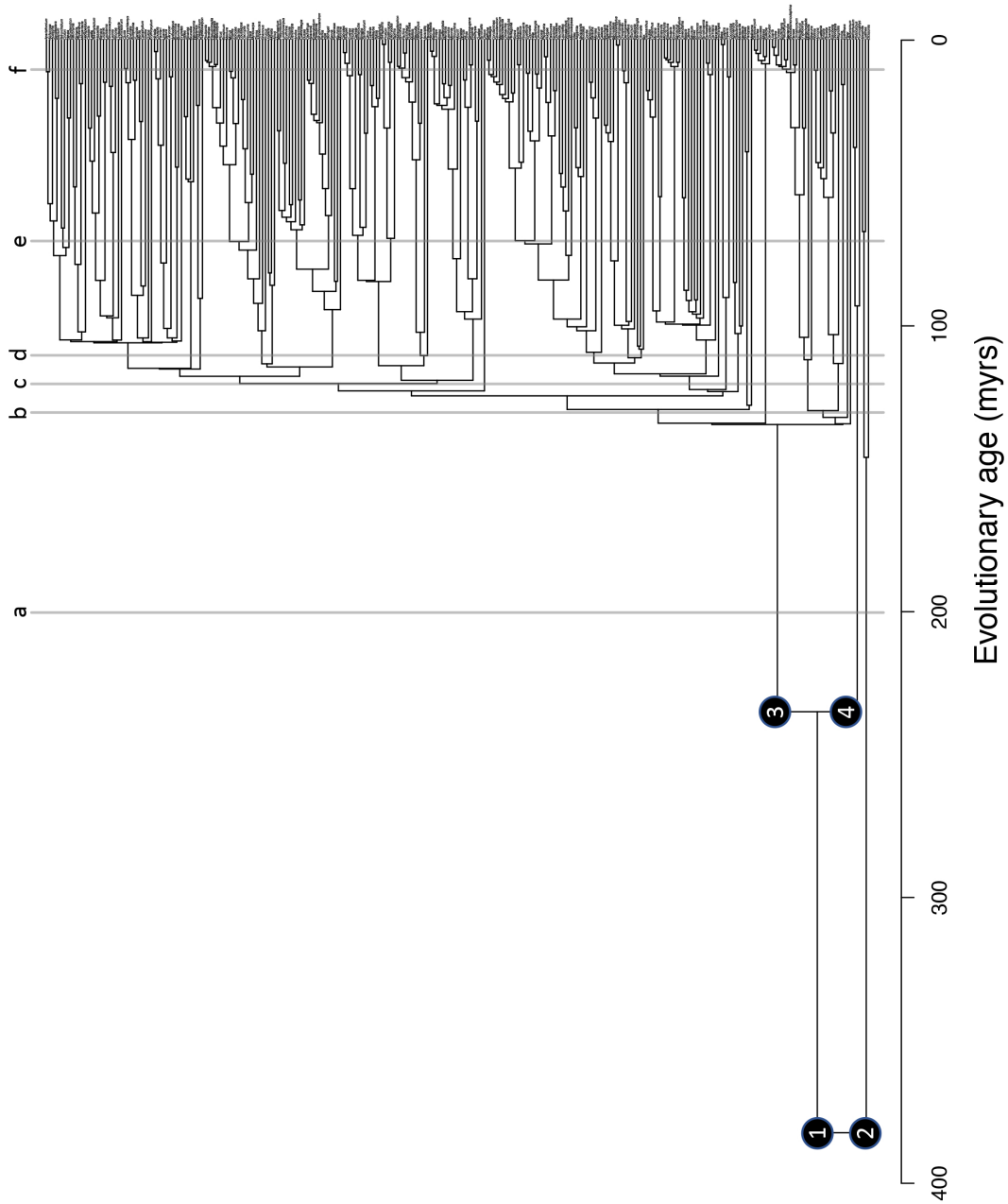

Figure 3.4: Genus level phylogeny for 275 genera occurring across 23 plots along an elevation gradient from 425 to 3625 m asl. Numbered nodes relate to lineages mentioned in the text: 1 = seed plants, 2 = tree ferns, 3 = angiosperms, 4 = gymnosperms. Grey vertical lines relate to evolutionary depths of 10, 70, 110, 120, 130, and 200 myrs with letters relating to the panels presented in Figure 3.5.

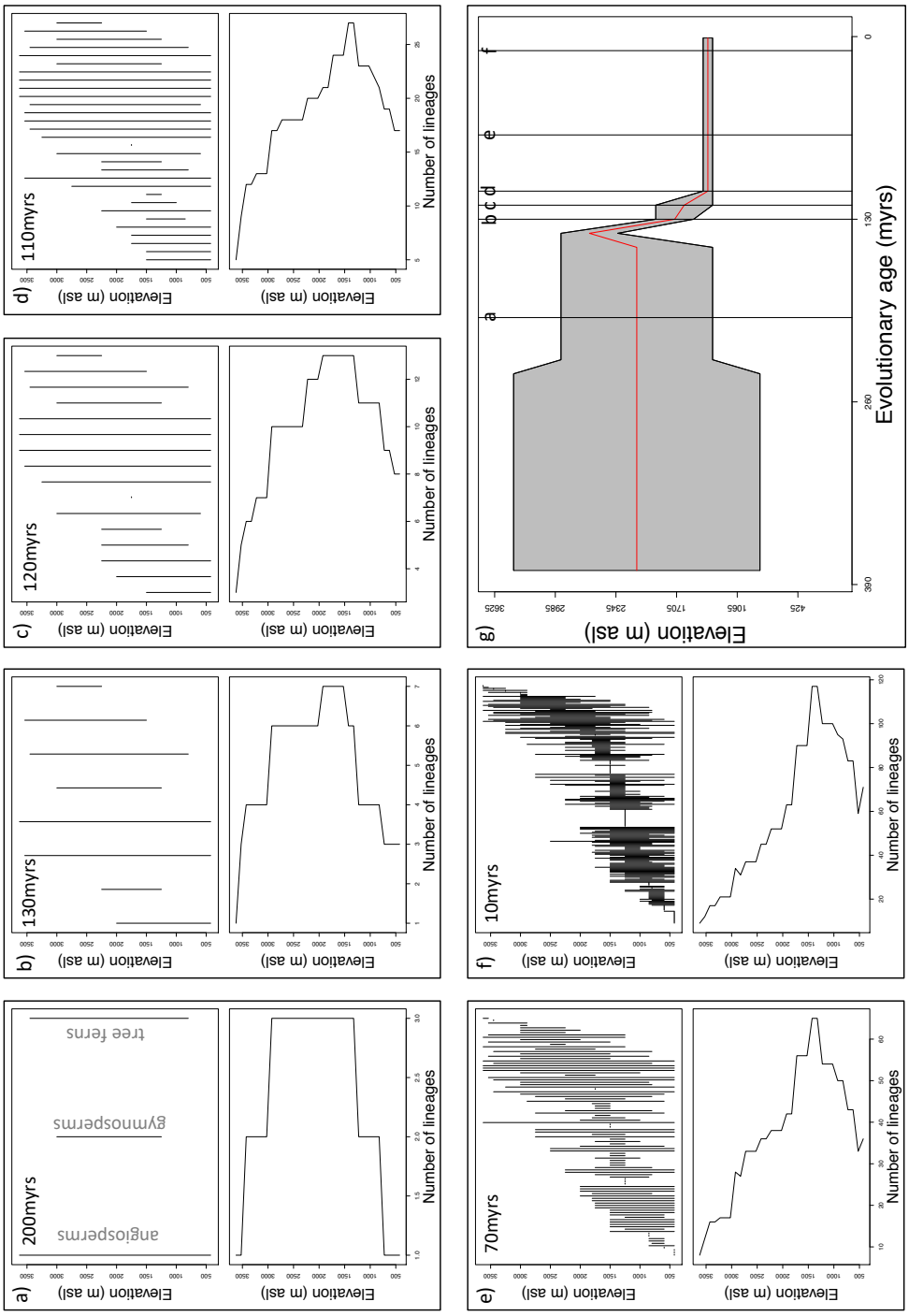

Figure 3.5: Panels a-f illustrate how evolutionary age structure varies across elevation and at six notable evolutionary depths a = 200 myrs, b = 130 myrs, c = 120 myrs, d = 110 myrs, e = 70 myrs, f = 10 myrs. Within each panel, the upper plot illustrates the elevational ranges of lineages. Vertical lines represent each individual lineage present at the respective evolutionary depth. Lower plots represent the number of lineages (x-axis) across elevation (y-axis) at each of the size evolutionary depths. Panel g illustrates how the elevations at which lineage richness is most numerous changes across different evolutionary depths. The grey shaded area represents the elevations most numerous in lineages across evolutionary depths. The red line illustrates mean elevation of the peak number of lineages. Vertical grey lines in g with letters relate to panels a-f.

= 27) is between 1300-1500 m asl (Figure 3.5g). At an evolutionary depth of 120 myrs (Figure 3.5c), there are 16 lineages that presently occur along the elevation transect. 1 of these lineages does not presently occur above 1750 m asl and 1 lineage does not occur below 1750 m asl. The peak in the number of 120 myr old lineages (n = 16) is between 1300-1900 m asl (Figure 3.5g). At an evolutionary depth of 130 myrs (Figure 3.5b), there are 8 lineages that presently occur along the elevation transect. None of these lineages are presently restricted below 1750 m asl and 1 lineage does not occur below 1750 m asl. The peak in the number of 130 myr old lineages (n = 7) is between 1500-2000 m asl (Figure 3.5g).

3.5 Discussion

We find a discernible contrast between taxonomic and phylogenetic richness patterns for trees across a tropical montane forest elevation gradient. Average genus richness is essentially invariant with elevation until 1376 m asl ($\pm$329m) above which it declines, while evolutionary richness clearly peaks at mid-elevations. This peak in evolutionary richness at intermediate elevations is driven by a greater number of older evolutionary lineages at mid to high elevations, as well as the fact that many relatively recently diverged lineages do not extend their distribution above 1500-1750 m asl. The results considering angiosperms only are similar, albeit the mid-elevation peak is not as pronounced (Figure 3.6). This demonstrates that while our findings are not solely driven by the increased presence of tree-fern and gymnosperm lineages at mid to high elevations, these lineages do exert a strong influence on evolutionary richness patterns. Overall, our results clearly show that the elevational diversity gradient within TMF, whether based on taxonomic or phylogenetic diversity, does not follow a simple linear decrease with increased elevation. Our findings do not support the idea that the TMF flora constitutes a recently derived and depauperate subset of lowland tropical diversity, as suggested by the Tropical Niche Conservatism and Out of the Tropics hypotheses (Wiens and Donoghue, 2004; Jablonski et al., 2006).

The elevational trend in average genus richness, showing a relatively invariant pattern up to mid-elevations and then falling steeply (Figure 3.2a), is consistent with trends for taxonomic richness previously recorded in neotropical forests, though these patterns were previously interpreted as a linear decrease given the absence of a lower elevation comparison (Gentry, 1988; Vazquez and Givnish, 1998). A fundamental factor in the general decrease in richness with elevation may be the well-established positive relationship between richness and area (MacArthur and Wilson, 1967; Rosenzweig, 1995). As one moves up a mountain gradient there is frequently a decline in the amount of land area available for taxa to occupy and as such richness declines. Yet, area-effects are unlikely to explain richness patterns alone (Rosenzweig, 1992). Firstly, our analyses are based on 1-hectare plots, thus actual sampling area is standardised. Secondly, taxonomic richness tends to be greater in heterogeneous environments (Kreft and Jetz, 2007; Antonelli et al., 2018). As such, the high environmental heterogeneity of montane environments, in combination with non-linear climatic gradients such a precipitation, may be driving the non-linear genus richness pattern we observe.

In contrast to the taxonomic richness trend, both evolutionary richness metrics, PD and TILD, show richness trends with a clear increase up to mid-elevations, and a subsequent decrease towards higher elevations. However, the shape of this trend varies between the two measures. PD displays a distinct mid elevation peak between c.1300-1500 m asl (Figure 3.2b). TILD follows a more gradual hump-shaped pattern across elevation, with the highest values observed across a range of middle elevations (Figure 3.2d). The different patterns described by these two metrics, associated to differential weighting of numbers of lineages at different evolutionary depths, illustrates variation in the evolutionary age structure of tree communities at different elevations, as further discussed below. TILD gives equal weight to diversity across all evolutionary depths of a phylogeny, while PD is more strongly correlated with the number of recently diverged lineages (Dexter et al., 2019). As such, PD displays an elevational richness pattern which might be seen as intermediate between those for genus richness and

TILD.

Meanwhile, the elevational pattern of sesPD, suggests a non-linear increase in richness with elevation, which only declines at the highest elevations sampled (Figure 3.2c). This pattern is likely driven by the strong correlation of sesPD with the number of lineages in deep evolutionary time (Dexter et al., 2019), which are more prevalent at middle and high elevations. Richness calculations using sesPD may give older lineages an exaggerated weight; thus, interpretation of such patterns should be made with caution. It has been shown that variation in standardised phylogenetic diversity metrics may be an artefact of variation in taxonomic richness (Sandel, 2018). Further, as an estimator of the richness dimension of diversity, sesPD may in reality be rather poor (Tucker et al., 2017; Dexter et al., 2019).

Deeper investigation into the evolutionary age of tree lineages across elevation reinforces, and further explains, the trends revealed by different richness metrics. The greater number of older lineages occurring at higher elevations is revealed by the changing number, and distribution pattern, of lineages at different evolutionary depths (Figure 3.5a-f.). The elevational ranges of lineages at younger evolutionary depths (Figure 3.5e-f) indicate that 53% of the lineages (n = 125) that are younger than 10 million years are not found above 1750 m asl, and 33% of lineages (n = 33) that are younger than 70 million years, are not found above 1750 m asl. Deeper in evolutionary time, the number of lineages is greater at higher elevations and indeed there are no lineages older than 130 million years restricted to a distribution below 1750 m asl. Between evolutionary depths of 110-130 million years there is a discernible shift in the elevation of peak number of lineages. For lineages that are 130 million years old the highest number of lineages occurs between 1500-2000 m asl, but for lineages that are 110 million years old the elevation where the highest number of lineages occur is lower, between 1300-1500 m asl (Figure 3.5g). This evolutionary time period is congruent with the diversification of eudicot lineages c.120-130 million years ago (Magallón et al., 2015). If many eudicot lineages diversified at mid to low elevations, it may explain the changing elevations of maximum number of lineages. These observations are

consistent with previous findings suggesting a positive correlation between elevation and evolutionary age, as quantified by mean family ages (Segovia et al., 2013; Tiede et al., 2015). However, we suggest our analysis based on phylogenetic depth may be more evolutionarily meaningful than ages of taxonomic families, which are dependent on the vagaries of circumscription by taxonomists.

Our results do not support the predictions of the Tropical Niche Conservatism or Out of the Tropics hypotheses, which assume that the flora of higher elevations is essentially an evolutionarily younger, less diverse subset of that found in the tropical lowlands (Wiens and Donoghue, 2004; Jablonski et al., 2006). Where TNC and OTT predict decreasing evolutionary richness with elevation, we find mid-elevations are home to greater evolutionary richness than high or low elevations. Where TNC predicts a decline in evolutionary age with elevation, we find mid and high elevations to be home to a greater number of older lineages, while many younger lineages do not extend above middle elevations.

The mid-elevation peak in evolutionary richness maybe be explained by a montane flora which is evolutionarily distinct to that found in the lowlands (Segovia and Armesto 2015; also see Chapter 2). It has previously bee demonstrated that within the Tropical Andes, the three major biomes of seasonally dry topical forest, mesic mid-elevation montane forest, and high-elevation grassland, contain floras with separate evolutionary histories (Särkinen et al., 2012). The suggestion that species may find it easier to migrate to new habitat matching their present niche, rather than adapt to novel conditions (Edwards and Donoghue, 2013) may underlie such patterns. Indeed, work conducted in Borneo on Mt. Kinabalu, has revealed a montane diversity largely composed of pre-adapted immigrant lineages, though mixed with the descendants of lowland ancestors (Merckx et al., 2015). During the Andean uplift of the Neogene, many tree species colonising this new habitat may have come from extra-tropical lineages already adapted to the montane environment. For example, the Cunoniaceae family may have extra-tropical evolutionary origins (Poole et al., 2000) and contains genera, such as *Weinmannia*, which are abundant at high elevations in the tropics. With rep-

resentatives from both the lowland tropical flora and the montane extra-tropical flora, mid-elevations might be expected to display the high evolutionary diversity we observe.

A complementary influence on the mid-elevation peak in diversity may be the presence of the cloud-base ecotone. Although evidence is mixed, ecotones are hypothesised to display higher biological diversity than adjoining areas (Odum and Odum, 1963; Risser, 1995) and may act has important generators of diversity (Moritz et al., 2000). Ecotonal areas might have increased diversity due to mass effects, the occurrence of species outside their core habitat (Shmida and Wilson, 1985). A few individuals from species which are self-maintaining in adjacent habitat may 'leak' into ecotonal areas, increasing their richness. For example, across an elevation gradient in the Canadian Rockies, higher diversity was recorded at the alpine/subalpine ecotone (Kernaghan and Harper, 2001). Along our gradient, the transition from lower montane forest into cloud forest, around 1500-2000 m asl, comprises the cloud-base ecotone (Rapp and Silman, 2012; Fadrique et al., 2018). The cloud-base, and the substantial environmental changes in precipitation, diurnal temperature range (Rapp and Silman, 2012), and solar radiation (Fyllas et al., 2017) that occur there, are likely to exert influence on the composition and distribution of tree lineages. Our results show these middle elevations as the areas of highest evolutionary richness within TMF. The cloud-base may represent a 'leaky barrier' where a mix of representatives from both the montane flora above, and the lowland flora below are able to occur, boosting evolutionary diversity.

It is likely that other, broader factors also shape elevational richness patterns within TMF. For example, mid-elevations around 1700 m asl may simply represent the elevational limits of those taxa from lowland Amazonian communities that adapted to a cooler climate during the Pleistocene (Silman, 2007). Perhaps through evolutionary adaptation, these taxa are able to persist in present day cool mid-elevation climate, yet temperatures above c.1700 m asl may be cooler than Quaternary conditions in the lowlands, and therefore beyond the tolerances of these lowland taxa. Such a general elevational limit may be consistent with our observations of a relatively large number

of younger lineages occupying elevational distributions that do not reach above 1500-1750 m asl and may in part explain mid-elevation richness patterns.

Our results show that the richness pattern of trees along a tropical montane forest elevation gradient depends substantially upon the dimension of richness quantified. We demonstrate clear contrasts between taxonomic and evolutionary richness patterns, as well as variation in the richness pattern across evolutionary depths. The pattern of evolutionary richness along this elevation gradient, and the observed tendency for older lineages to be found at mid-high elevations, are not consistent with the predictions of the Tropical Niche Conservatism and the Out of the Tropics hypotheses. Rather we suggest these patterns support the notion of a mid-elevation mixing ground, between a tropical montane flora and a tropical lowland flora, which have distinct evolutionary histories. Such a pattern may have important implications for our understanding of how biodiversity is distributed across tropical montane landscapes. In conservation terms, the pattern of high evolutionary diversity of mid-elevations, within TMF, shows what stands to be lost should global environmental change substantially alter this unique system, for example by shifting the cloud-base (Helmer et al., 2019). Lowland Amazonia is traditionally considered to contain the most diverse forests on the planet (Henderson et al., 1991; Myers et al., 2000), yet we reveal a pattern suggesting that the richness of mid-elevation montane forests could rival that of the lowlands, especially when factoring in the full evolutionary depth of lineages.

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3.A Appendix

Table 3.3: Angiosperm data only - comparison of regression model fits for elevational patterns of genus richness, phylogenetic diversity (PD), standardised effect size phylogenetic diversity (sesPD), and time-integrated lineage diversity (TILD). Numbers in bold indicate highest model R^2 value for each diversity measure.

	Linear regression		**Quadratic regression**		**Breakpoint regression**	
	R^2	**p-value**	**R^2**	**p-value**	**R^2**	**p-value**
Genus richness	0.87	<0.001	0.87	<0.001	**0.89**	na
PD	0.85	<0.001	0.89	<0.001	**0.93**	na
sesPD	0.37	0.001	0.46	<0.001	**0.51**	na
TILD	0.84	<0.001	0.95	<0.001	**0.96**	na

Table 3.4: Angiosperm only data - summary of lineage elevational range trends and richness at five notable evolutionary depths.

Evolutionary depth (myrs)	**Total no. lineages**	**No. lineages only <1750 m asl**	**No. lineages only >1750 m asl**	**Elevations of peak lineage richness (m asl)**	**No. lineages at richness peak**
10	232	124	15	1300-1500	114
70	97	32	8	1300-1500	63
110	27	4	0	1300-1500	25
120	13	1	0	1300-2000	11
130	5	0	0	1500-2000	5

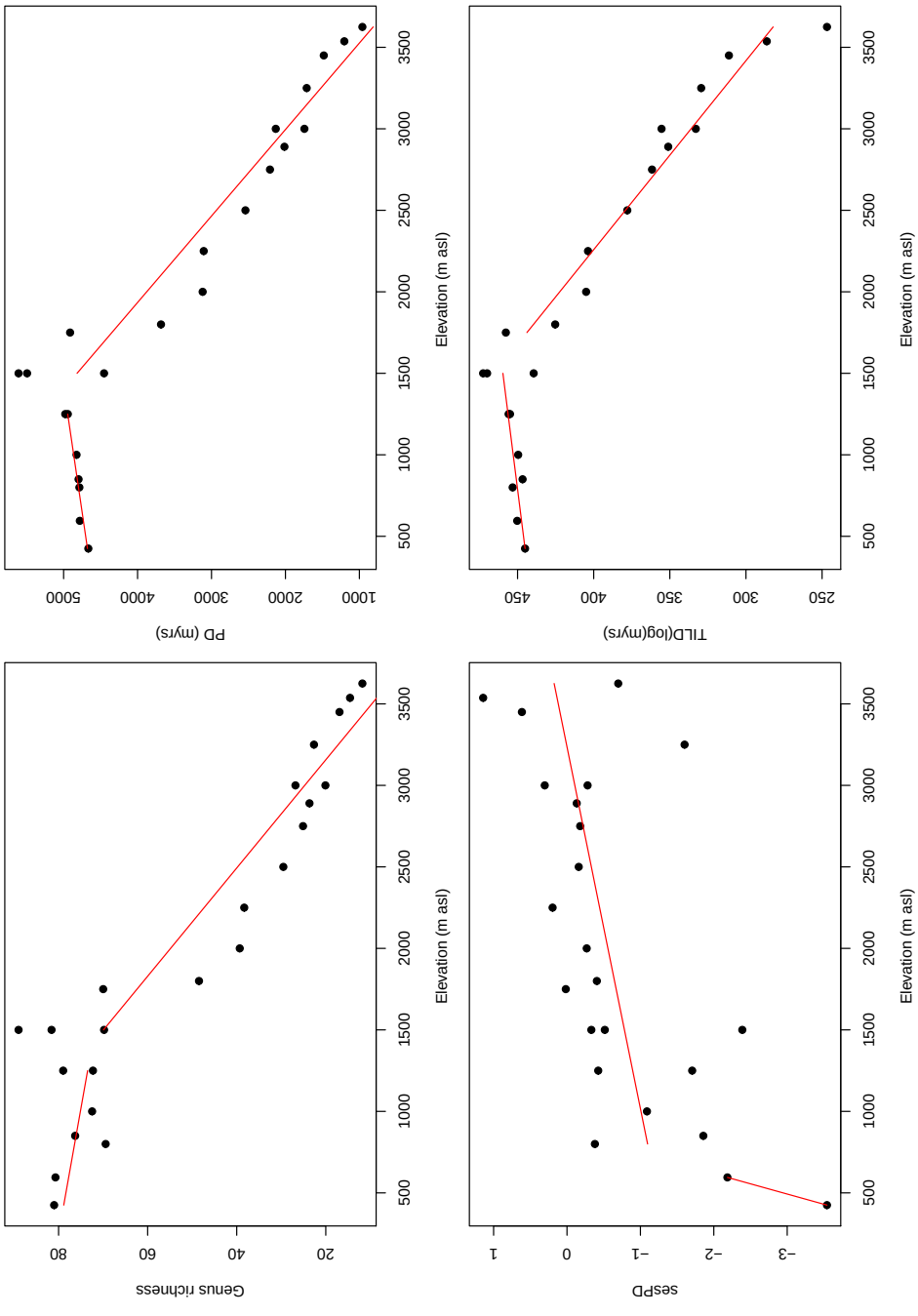

Figure 3.6: Angiosperm only analysis - the shape of the elevational richness gradient between metrics. **a)** Genus richness and **b)** phylogenetic diversity (PD) **c)** standardised effect size phylogenetic diversity (sesPD) and **d)** time integrated lineage diversity (TILD) are best described by breakpoint regression models. Points are mean rarefied metric values for each plot. Red lines represent regression lines from the best fitting model for each metric.

Chapter 4

Evolutionary trends in elevational diversity, distribution, and leaf trait patterns within the plant tribe Miconieae

4.1 Abstract

The mechanisms which underlie the elevational distribution of species are not fully understood. We focus on a tropical montane forest elevation gradient of $>$3000 m to consider potential evolutionary associations between functional trait trends and species elevational distributions within the plant tribe Miconieae. We additionally consider whether species-level patterns of diversity and distribution in Miconieae are consistent with broader trends at deeper taxonomic scales. We find trait trends such as decreasing SLA with increasing elevation, and a tendency for closely related species to have similar trait values. Narrow elevational ranges predominate, with 96% of species being found over $<$1000 m, and closely related species tend to occur at similar elevations. Observed patterns may represent correlated evolution between species' trait strategies and elevational occurence. We additionally find species and evolutionary richness within Miconieae up to $\sim$ 2000 m asl is equivalent or higher than that found at lower elevations $\sim$ 500 m asl. The species-level elevational diversity trend in Miconieae reflects the general patterns observed across vascular plants at deeper taxonomic levels. The consistency of trends across taxonomic scales suggests evolutionary constraint on species' trait strategies, elevational distributions, and the evolutionary association of the two, may be ubiquitous across plants within tropical montane forests

4.2 Introduction

Understanding patterns and drivers of variation in the distribution and diversity of taxa across different environments is a core theme within ecology. Establishing whether such trends hold as tractable and general rules across scales has long been a prominent goal for ecologists (Levin, 1992; McGill, 2019; Rapacciuolo and Blois, 2019). Here we take an evolutionary perspective on woody plant diversity and distribution patterns along a tropical montane forest elevation gradient. We focus on the plant tribe Miconieae (Melastomataceae) and consider whether species level trends within this lineage are consistent with broader, genus-level community trends. In addition,

we examine elevational trends in functional leaf traits, and consider whether trait patterns and their evolutionary associations mechanistically explain species elevational distribution limits.

Globally, elevation gradients are associated with substantial environmental changes, such variations in temperature, precipitation and soil systems (Körner, 2007; Rapp and Silman, 2012; Nottingham et al., 2018), along with notable ecological trends, such as diversity gradients and taxonomic turnover (Malhi et al., 2010; Jankowski et al., 2013; Baldeck et al., 2016). Across the specific TMF elevation gradient under consideration, diversity trends suggest that the genus-level taxonomic and evolutionary richness of mid-elevation montane forest is as high or higher than that found at lower elevations (Chapter 3). Further, elevational distribution patterns are in part constrained by the evolutionary tendency for closely related genera to occur at similar elevations (Chapter 2). Yet a few genera, such as *Miconia* (Melastomataceae), *Meliosma* (Sabiaceae) and *Ocotea* (Lauraceae), appear to escape evolutionary conservatism and occupy a large elevational range, spanning broad environmental variation (Chapter 2). It is less apparent whether such wider community-level trends are echoed within individual lineages.

The nature of patterns within ecology is frequently contingent on the spatial, temporal, or taxonomic scale of study (Levin, 1992; Simberloff, 2004; Vellend, 2010). Where species level identifications are difficult or not readily obtainable, such as within tropical systems (Dexter et al., 2010), it is not uncommon for higher taxonomic levels such as families or genera to be used as the scale of analysis (Gaston and Williams, 1993; Ricotta et al., 2002; Coelho de Souza et al., 2016; Dexter and Chave, 2016). However, such approaches are not without problems. Across taxonomic scales, groupings within a given hierarchical level, such as family or genus, may not be equivalent. For example, the vagaries of circumscription may lead to large variation in the diversity represented by taxonomic groupings. A genus may contain a single species, or it may contain thousands (Sigwart et al., 2018). As such, a genus-level comparison of functional trait variation for example, including a genus of a thousand species and genus

of a single species, may be of debatable utility.

A further problem, particularly in tropical systems, is the paraphyletic nature of a number of diverse genera such as *Miconia* (Melastomataceae; Michelangeli et al. 2004), *Pouteria* (Sapotaceae; Swenson and Anderberg 2005), and *Protium* (Burseraceae; Weeks et al. 2005). Phylogenetically, these genera have other genera nested within them. In the case of *Miconia*, genera such as *Leandra* and *Tococa*, are nested within the broader clade. Therefore, in evolutionary terms, a given species of *Miconia* may be more closely related to a species of *Leandra* or *Tococa* than it is to another *Miconia* species. Such taxonomic irregularities could clearly effect analysis and interpretation of ecological and evolutionary patterns. Using higher level taxonomic data when applying evolutionary analyses may be problematic. Indeed, it has been demonstrated that genus-level data and analyses can be misleading in large-scale evolutionary studies (Smith and O'Meara, 2009).

We focus on the plant tribe Miconieae (Melastomataceae) in order to examine whether species-level elevational patterns of diversity and evolutionary constraint on distribution match those observed along our TMF elevation gradient at the genus-level (Chapters 2 and 3). Miconieae (sensu stricto; Michelangeli et al. 2004) is a hyperdiverse neo-tropical lineage of 30 genera, containing c.2200 species of predominantly shrubs and small trees (Michelangeli et al., 2004). The Melastomataceae family is found from lowland rain forest to high-elevation shrub communities (Reginato and Michelangeli, 2016). Within Miconieae, the genus Miconia is exceptional in its elevational distribution occurring across the full elevational range of the gradient under study (see Chapter 2). The Melastomataceae family more generally is a key component of tropical montane forest diversity (Gentry, 1988; Homeier et al., 2010). The diversity and broad elevational range of Miconieae, makes it an ideal lineage to examine whether genus-level elevational richness patterns and evolutionary conservatism of distribution within TMF match species-level trends.

In addition to a lack of clarity over the generality of evolutionary conservatism for

elevational distributions across taxonomic scales, a mechanistic explanation for the pattern is incomplete. Environmental conditions, such as temperature and precipitation, are thought to impose a filter on the composition of a given community (Kraft et al., 2015). Only species with the necessary adaptations or functional traits are able to pass through this environmental filter and establish within the community. Such environmental filtering, in combination with evolutionary conservatism leads to the expectation that closely related lineages will occur in similar environments because they possess similar adaptations or traits. Environmental filtering is thought to be strongest in harsh environments, such as the low temperatures found at high elevation (Chase, 2007; Marx et al., 2017). Therefore, along a TMF elevation gradient, if phylogenetic conservatism of elevational distribution holds at the species level, we would expect to find clustering of closely related species at similar elevations with similar functional traits. Alternatively, theory around competitive exclusion, the process whereby species which are too similar are unlikely to co-occur (Macarthur and Levins, 1967), would suggest species-level patterns may deviate from genus-level trends. For example, a classic study of the Floridian oak (*Quercus*) community found co-occurring species to be more distantly related than expected by chance (Cavender-Bares et al., 2004). Further, general trait patterns are not always reflected within individual species or lineages (Ackerly and Cornwell, 2007).

Functional traits are considered to be representative of species eco-physiological strategies (Westoby et al., 2002) and act as good predictors of plant performance in tropical trees (Poorter and Bongers, 2006). The global leaf economic spectrum is a well-established concept, placing a number of leaf traits in the context of a continuum of fast to slow ecological strategies (Wright et al., 2004) and represents a major axis of plant form and function (Reich, 2014; Díaz et al., 2016). Leaf traits such as specific leaf area (SLA), the ratio of leaf area to leaf dry mass, and its inverse, leaf mass per area (LMA), are widely measured traits associated with the productivity and competitive ability of plants (Poorter et al., 2009; Bruelheide et al., 2018). The link between functional traits and eco-physiological strategies means that investigation of

leaf trends across the environmental variation of elevation, and evolutionary associations between traits and species distributions, may yield a mechanistic explanation for the occurrence of closely related taxa at similar elevations.

Variation in functional trait patterns across different environments is well documented (Cornwell and Ackerly, 2009; Swenson, 2011; Reich, 2014; Wright et al., 2017). As a general rule, fast growing, resource-acquisitive species invest in short lived leaves with high SLA values and tend to be more competitive in productive habitats such as wet and warm lowland tropical rainforests. In contrast, slow growing, resource-conservative species invest in tough and durable leaves with low SLA values and tend to have a competitive advantage in unproductive habitats such as cold high elevation environments (Poorter et al., 2009; Wright et al., 2017). Across tropical montane environments the expected trend for fast, resource-acquisitive species at lower elevations and slow, resource-conservative species at higher elevations has been observed (Swenson, 2011; Read et al., 2014; Asner and Martin, 2016). More specifically, a general trend of decreasing SLA with increasing elevation has been recorded along our TMF elevation gradient of focus (van de Weg et al., 2009).

Functional trait patterns are influenced by evolutionary processes (Reich et al., 2003; Kraft and Ackerly, 2010). Because evolutionarily close relatives tend to be ecologically similar, functional trait values are expected to show phylogenetic signal (Freckleton et al., 2002; Ackerly, 2009). Indeed, among tropical trees, numerous studies have demonstrated phylogenetic signal for traits such as leaf structure and chemistry, wood density, seed mass, tree size, and growth rate (Baraloto et al., 2012; Yang et al., 2014; Coelho de Souza et al., 2016). Within the Melastomataceae family, recent work along a Costa Rican elevation gradient found decreasing SLA and leaf size with elevation but mixed evidence for conservatism of traits, finding phylogenetic signal for leaf size, leaf dry matter content (LDMC) and leaf force to puncture, but no signal for SLA or leaf nitrogen content (Kandlikar et al., 2018). However, this Costa Rican study reached a maximum elevation of 2500 m asl, meaning evolutionarily distinct high elevation clades with particular trait strategies may have been missed. Meanwhile, sam-

pling was also absent between 800-2000 m asl, thereby missing the mid-elevations where the highest levels of diversity may occur, if species trends are similar to the general genus-level pattern. Additional investigation of the trait trends of Miconieae within TMF is warranted, and a more complete understanding of elevational patterns will enable us to put the resource-investment strategies of Miconieae species into the context of the broader, global leaf trait spectrum. Further, an explicit examination of the potential association between the evolution of functional leaf traits and species elevational distributions has yet to be conducted.

Amongst the general pattern for evolutionarily constrained, narrow elevational ranges (see Chapter 2), lineages such as Miconieae, which escape this constraint and occupy a broad elevational range, may seem exceptional. Yet, if general patterns are reflected within such lineages at the species scale, they may simply be the exceptions that prove the rule. Additionally, we may detect functional trait patterns that associate with the evolution of constrained distributions. Alternatively, if Miconieae species do not follow general elevational trends, we may detect a greater lability for functional traits than has been recorded in most tropical tree lineages, where evidence for phylogenetic signal in leaf traits is prevalent. By testing for potential associations in the evolution of leaf traits and elevational occupancy within Miconieae, we will gain deeper insight into the drivers of distribution patterns across TMF. Evolutionary conservatism for functional traits may be a limiting factor on species' elevational distributions. Understanding elevational patterns within Miconieae will improve our understanding of the role individual lineage play in shaping broader trends. Here we explicitly investigate three main questions: 1) Do elevational diversity patterns and phylogenetic constraint on elevational distribution within Miconieae match genus scale trends? 2) Is there phylogenetic signal for leaf traits within Miconieae? 3) Is there an association between the evolution of leaf traits and species elevational distributions?

4.3 Methods

4.3.1 Study site

This study is based on an Amazon-Andes elevation gradient within tropical montane forest from 531 to 3710 m asl, centred on the Kosñipata valley, both within and near Manu National Park, south-eastern Peru (Figure 4.1). Ranging from lowland/submontane forest, up to the tropical montane forest-puna grassland transition, the gradient encompasses large environmental and habitat variation. From around 1500-2000 m asl and upwards frequent and prolonged cloud immersion are the characteristic climatic feature of tropical montane cloud forest (Girardin et al., 2010; Rapp and Silman, 2012). Mean annual temperatures range from c.24°C at low elevations to c.9°C at higher elevation (Malhi et al., 2017). Mean total annual precipitation rises from c.3000 mm yr^{-1} at low elevation to c.5000 mm yr^{-1} at around 1000 m asl, then declines monotonically to c.1000 mm yr^{-1} at high elevation (Rapp and Silman, 2012).

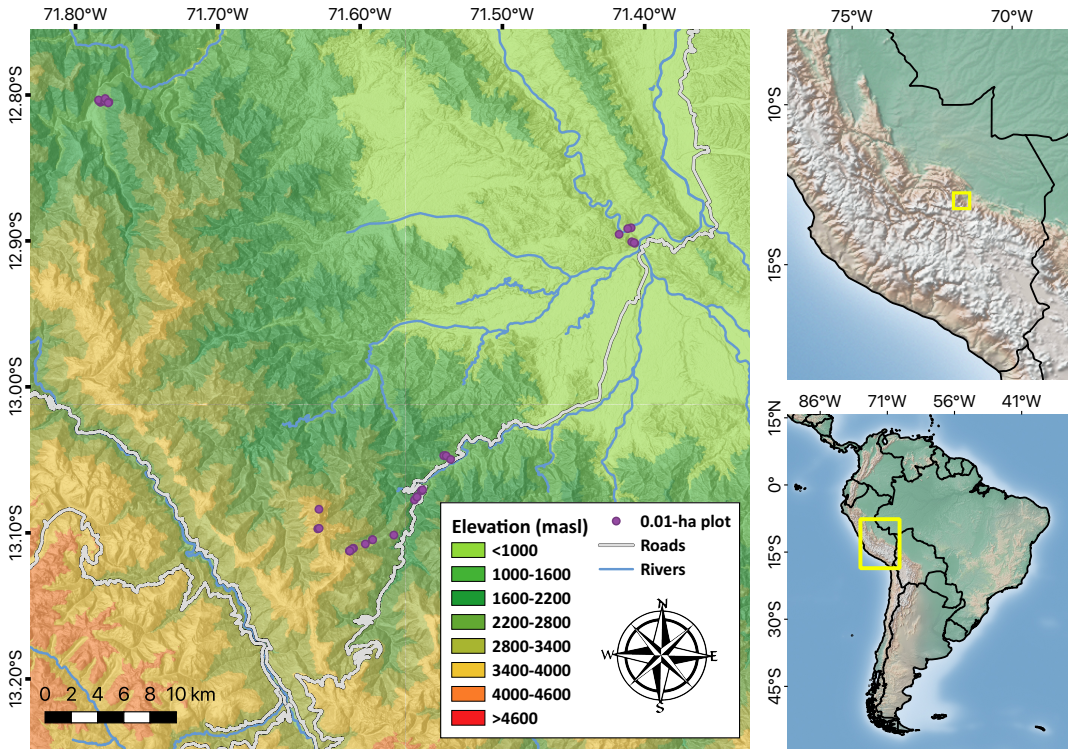

Figure 4.1: Location of 41 0.01-ha plots along an elevation gradient on the Amazonian flank of the south-eastern Peruvian Andes. Purple circles indicate location of plots.

4.3.2 Sampling

We set up 41, 0.01-ha (10m x 10m) plots distributed from 531 to 3645 m asl, with 3 plots set approximately every 300 m. Within each plot we sampled all Miconieae individuals $\geq$ 1cm DBH (diameter at breast height: = 130 cm above the ground; DBH). In a few instances, individual collections were also made outside plots, particularly for samples occurring above the treeline, with species sampled in proportion to their abundance, and with collections up to 3710 m asl. For each individual, we recorded DBH and height. We made two herbarium voucher specimens per individual (collections are currently held at E, MOL, and NY herbaria) and collected leaf material preserved in silica gel for subsequent DNA extraction.

4.3.3 Trait measurement

We collected three fully expanded, healthy leaves from each individual. Leaf material was kept moist then weighed for fresh weight soon after collection, using portable precision digital scales (SmartWeight, accuracy = $\pm$0.001g). For each leaf we measured leaf thickness at three points across the lamina (digital micrometer, DML). We determined leaf area by taking a digital image of each flattened leaf and analysing lamina area. We dried leaf material in silica gel until each sample reached constant mass (van de Weg et al, 2012) and weighed to allow calculation of leaf dry matter content (LDMC, mg g^{-1}) and specific leaf area (SLA, mm^2 mg^{-1}), following standard calculations (Perez-Harguindeguy et al., 2016).

4.3.4 DNA isolation, sequencing, and botanical identification

We homogenised silica-dried leaf material (TissueLyser II, Qiagen) and isolated genomic DNA from silica dried leaf material using cetyl-trimethylammonium bromide (CTAB), following standard procedures (Doyle and Doyle, 1990). Isolated DNA was amplified through polymerase chain reaction (PCR) and sequenced for the internal transcribed spacer region of ribosomal DNA (nrITS), and for the plastid spacer psbK-psbL. Sequencing reactions were completed by Edinburgh Genomics. We conducted

quality control, editing, and sequence assembly in Sequencher (v5.4). We identified samples to species, or morpho-species if a named identification was not possible, by comparing voucher specimens to herbarium collections, particularly those held by New York Botanical Garden (NYBG). We additionally compared the genetic sequences of samples with each other and with published sequences provided by taxonomic experts. Some identifications were made in consultation with Fabian Michelangeli at NYBG, the foremost expert on the taxonomy of Melastomataceae.

4.3.5 Phylogeny

We generated a phylogeny for the species found along the gradient by building a matrix of nuclear ribosomal spacers ITS1, ITS2, and ETS, and plastid intergenic spacers psbK-psbL and accD-psaI, which have all been widely used across the Melastomataceae (Goldenberg et al., 2015; Kriebel et al., 2015; Reginato and Michelangeli, 2016). Missing and additional ITS, ETS, and accD-psaI sequences for some named species, along with sequences for the Merianieae outgroup, were provided by Fabian Michelangeli at NYBG. We conducted sequence alignment using the MAFFT version 7 online service (https://mafft.cbrc.jp; Katoh et al. 2017) and manually checked and trimmed sequence 'ragged ends' in Mesquite v3.6 (Maddison and Maddison, 2018). We input the aligned sequence matrix into BEAST2 (Bouckaert et al., 2014) to perform Bayesian phylogenetic analysis and temporally calibrate the phylogeny. We ran two independent analyses of 100 million generations under the following settings: General Time Reversible (GTR) plus GAMMA model of sequence evolution, relaxed log normal molecular clock, and a Birth/Death prior for tree branching. A secondary crown age calibration prior for Miconieae (sensu Michelangeli et al. 2004) was set at 15 myrs, based on an estimate in Berger et al. (2016). We sampled every 10,000 generations and used Tracer v1.7.1 (Rambaut et al., 2018) to visually inspect convergence of Markov chain Monte Carlo (MCMC) and ensure an effective sample size $\geq$ 200 for all parameters. TreeAnnotator v2.5.2 was used to summarise output trees into a maximum clade credibility (MCC) tree (Figure 4.6), after a burn in of 50% of the output.

4.3.6 Elevational diversity trends

We calculated species richness as the number of species present in each plot. We calculated the evolutionary richness of each plot using both the phylogenetic diversity (PD; sensu Faith 1992) and the time integrated lineage diversity (TILD; Dexter et al. 2019) metrics. PD is calculated by summing the branch lengths of a phylogeny for taxa within a community, and includes the root stem (Faith, 1992), TILD is calculated by log-transforming the y-axis of a lineage through time plot (sensu Yguel et al. 2016), then integrating the area underneath the number of lineages line (Dexter et al., 2019). PD was calculated using the 'picante' package (Kembel et al., 2010), TILD was calculated using a new function published in Dexter et al. (2019). To investigate potential variation in the shape of the elevation richness pattern among metrics, we applied linear, quadratic, and breakpoint regression models to the plot metric values. We established the best fitting model for each metric through a comparison of R^2 values. Linear and quadratic regression were conducted using the 'lm' function in R package stats (Team, 2018). Breakpoint regressions were conducted using the 'segmented' function in the R package segmented (Muggeo, 2008).

4.3.7 Distribution trends, trait patterns, and evolutionary associations

To analyse species distribution trends, we calculated the mean elevational occurrence of each species along with their elevational range. We also calculated species mean trait values for SLA, LDMC and leaf thickness. Prior to analysis, trait values were log-transformed to improve normality of residuals. We estimated the level of phylogenetic signal for species elevational distributions and trait values using Pagel's λ (Pagel, 1999; Freckleton et al., 2002). λ is based on a comparison of tree branch length transformations, and contrasts variance in observed trait values against expected trait variance under a Brownian motion (BM) model of evolution. Values of λ around 0 indicate no phylogenetic signal. Values of λ around 1 indicate strong phylogenetic signal, matching that expected under a Brownian model of evolution. Values of λ between 0 and 1 indicate intermediate levels of phylogenetic signal. In order to

test whether results display metric dependency, we also calculated phylogenetic signal using Blomberg's K (Blomberg et al., 2003).

To test for correlation between traits and elevation, we conducted linear regressions of species mean trait values against species mean elevation. If one or more variables in a correlation display phylogenetic signal, it is possible that the correlation may be an artefact of interspecific autocorrelation due to phylogenetic relationships (Felsenstein, 1985). Therefore, we conducted phylogenetic generalised least squares analyses (PGLS; 'pgls' function in R package caper Orme et al. 2013) to investigate if trait elevational trends hold once phylogenetic relationships have been accounted for. PGLS analyses can also indicate whether two variables potentially evolved together under correlated evolution, i.e. evolutionary changes in one variable matched by evolutionary changes in the other. Thus, we additionally use PGLS to investigate whether species leaf trait and elevational distribution have evolved together. For species distribution, trait pattern, phylogenetic signal, and PGLS analyses, we used data from species sampled within plots (n = 83), plus additional species only found outside of plots (n = 5), with sampling of species outside plots proportional to abundance.

4.4 Results

4.4.1 Elevational diversity trends

Across all 41 plots a total of 447 individuals were collected belonging to 88 species. The most abundant species are Miconia sp.3 (n = 26), *Miconia spennerostachya* (n = 25), and *Miconia brachyanthera* (n = 22). The highest recorded species richness (n = 12) occurs in a plot at 1895 m asl (Figure 4.2a). The highest PD value (= 70.2 (myrs); Figure 4.2b) and TILD value (= 20.6 (log(myrs)); Figure 4.2c) occur in a plot at 655 m asl. The shape of the elevational diversity trend for Miconieae is relatively consistent across both taxonomic and evolutionary diversity metrics (Table 4.1 and Figure 4.2). For species richness a breakpoint regression provides the best fit (R^2 = 0.26), with a trend of increasing richness up to an estimated breakpoint at 2417 m

asl ($\pm$290 m), above which richness decreases (Figure 4.2a). The elevational trend in PD, with highest values generally across mid-elevations, is equivalently well described by both a quadratic regression (R^2 = 0.39) and a breakpoint regression (R^2 = 0.38) with an estimated breakpoint at 1871 m asl ($\pm$326 m) (Figure 4.2b). Similarly for TILD, a quadratic regression (R^2 = 0.47) and breakpoint regression (R^2 = 0.47), equally provide the best fit for an elevational trend with highest values across middle elevations and an estimates breakpoint at 1776 m asl ($\pm$256m) (Figure 4.2c).

Table 4.1: Comparison of regression model fits for elevational patterns of genus richness, phylogenetic diversity (PD), and time-integrated lineage diversity (TILD). Numbers in bold indicate highest model R^2 value for each diversity measure.

	Linear regression		**Quadratic regression**		**Breakpoint Regression**	
	R^2	**p-value**	**R^2**	**p-value**	**R^2**	**p-value**
Species richness	0.08	0.04	0.23	0.003	**0.26**	na
PD	0.28	$<$0.001	**0.39**	$<$0.001	0.38	na
TILD	0.32	$<$0.001	**0.47**	$<$0.001	**0.47**	na

4.4.2 Distribution trends, trait patterns, and evolutionary associations

We find substantial species turnover across elevation within Miconieae, as illustrated by the mean elevational occurrence and elevational ranges of species (Figure 4.3). Species tend to occupy very narrow elevational distributions. 47% (n = 41) of Miconieae species along this transect were only found at a single elevational location, while only 3.4% (n = 3) species are distributed across an elevational range $>$1000m. We find significant phylogenetic signal for species mean elevation (λ= 0.84, p $<$0.001; Figure 4.4a-c), with closely related species tending to occupy similar elevations. Conversely, we do not find significant phylogenetic signal for elevational range size (λ $<$0.01, p = 1). For functional leaf traits we find significant phylogenetic signal for log SLA (λ = 0.80, p = $<$0.001, Figure 4.4a), log leaf thickness (λ = 0.40, p $<$0.001, Figure 4.4b), and log LDMC (λ = 0.88, p $<$0.001, Figure 4.4c). Phylogenetic signal is consistent across both Pagel's λ and Blomberg's K (Table 4.2).

We find variation in the elevational patterns of the different leaf traits measured (Figure 4.5). Species mean log SLA shows a negative correlation with species mean

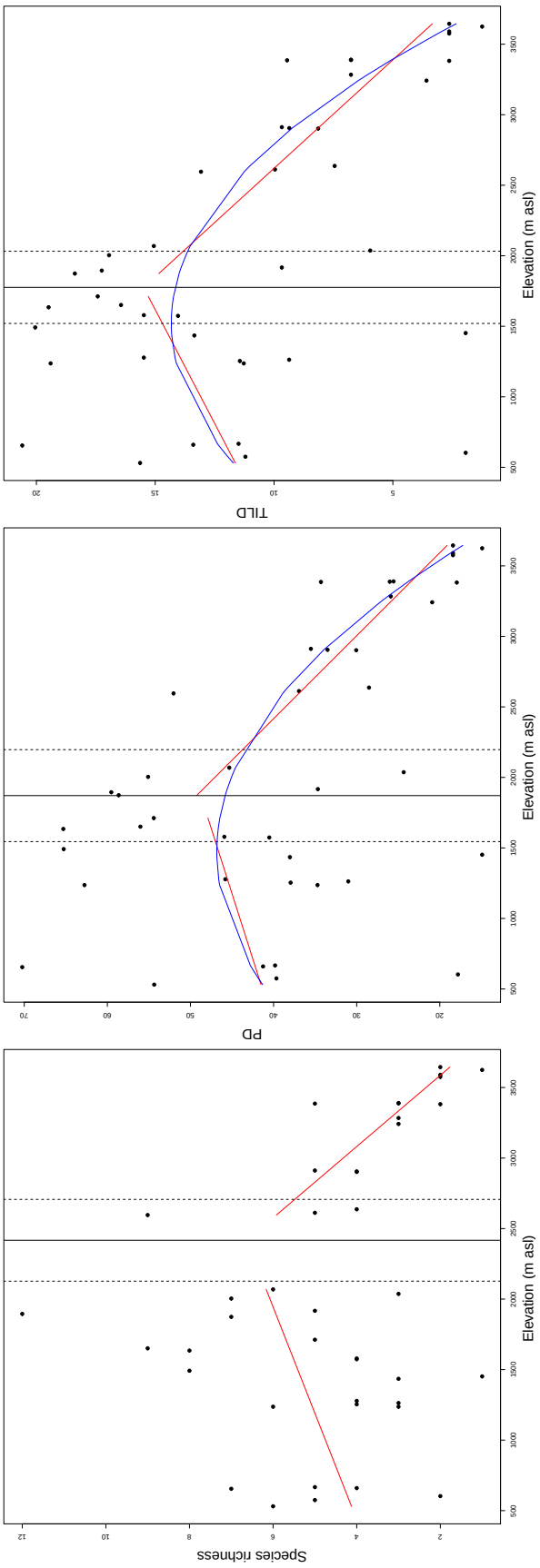

Figure 4.2: Miconieae diversity varies across plots (n = 41) along an elevation gradient from 531 to 3645 m asl **a)** The elevational pattern of species richness is best described by a breakpoint regression (R^2 = 0.26) with an estimated breakpoint at 2417 m asl ($\pm$290 m). **b)** The elevational pattern of PD is equally well described by both a quadratic regression (R^2 = 0.39) and a breakpoint regression (R^2 = 0.38) with and estimated breakpoint at 1871 m asl ($\pm$326 m). **c)** The elevational pattern of TILD is equally well described by both a quadratic regression (R^2 = 0.47) and a breakpoint regression (R^2 = 0.47) with an estimated breakpoint at 1776 m asl ($\pm$256 m). Points represent metric values of each plot. Solid blue lines represent quadratic regressions and solid red lines represent breakpoint regressions. Solid vertical lines indicate estimated breakpoints, with respective standard error represented by dashed vertical lines.

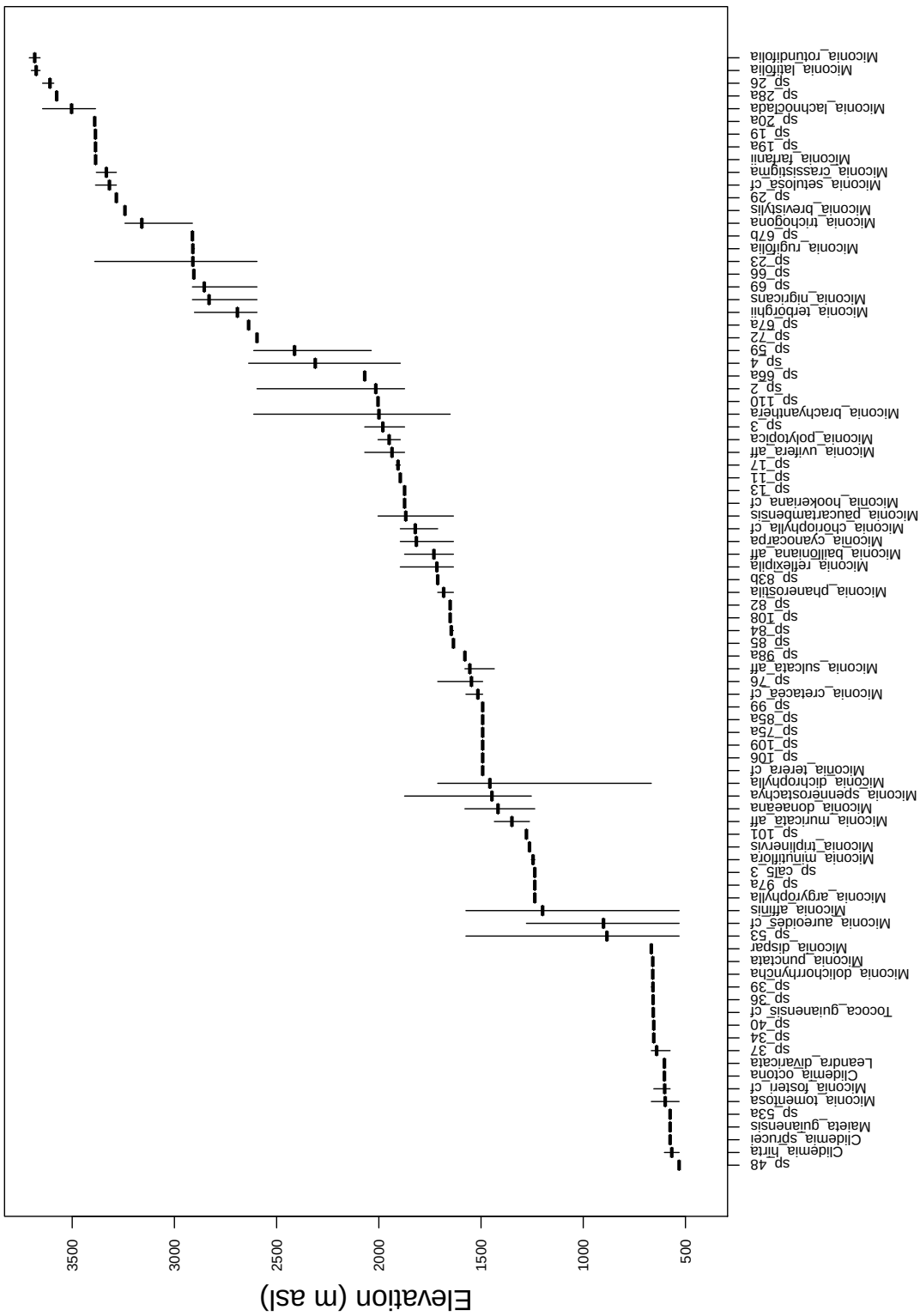

Figure 4.3: The plant tribe Miconieae displays complete species turnover across an elevation gradient from 531 – 3710 m asl. Species tend to have exceptionally narrow elevational ranges, with 47% of species only found at a single elevation. Thick bars indicate species mean elevation. Vertical lines indicate species elevational range sizes.

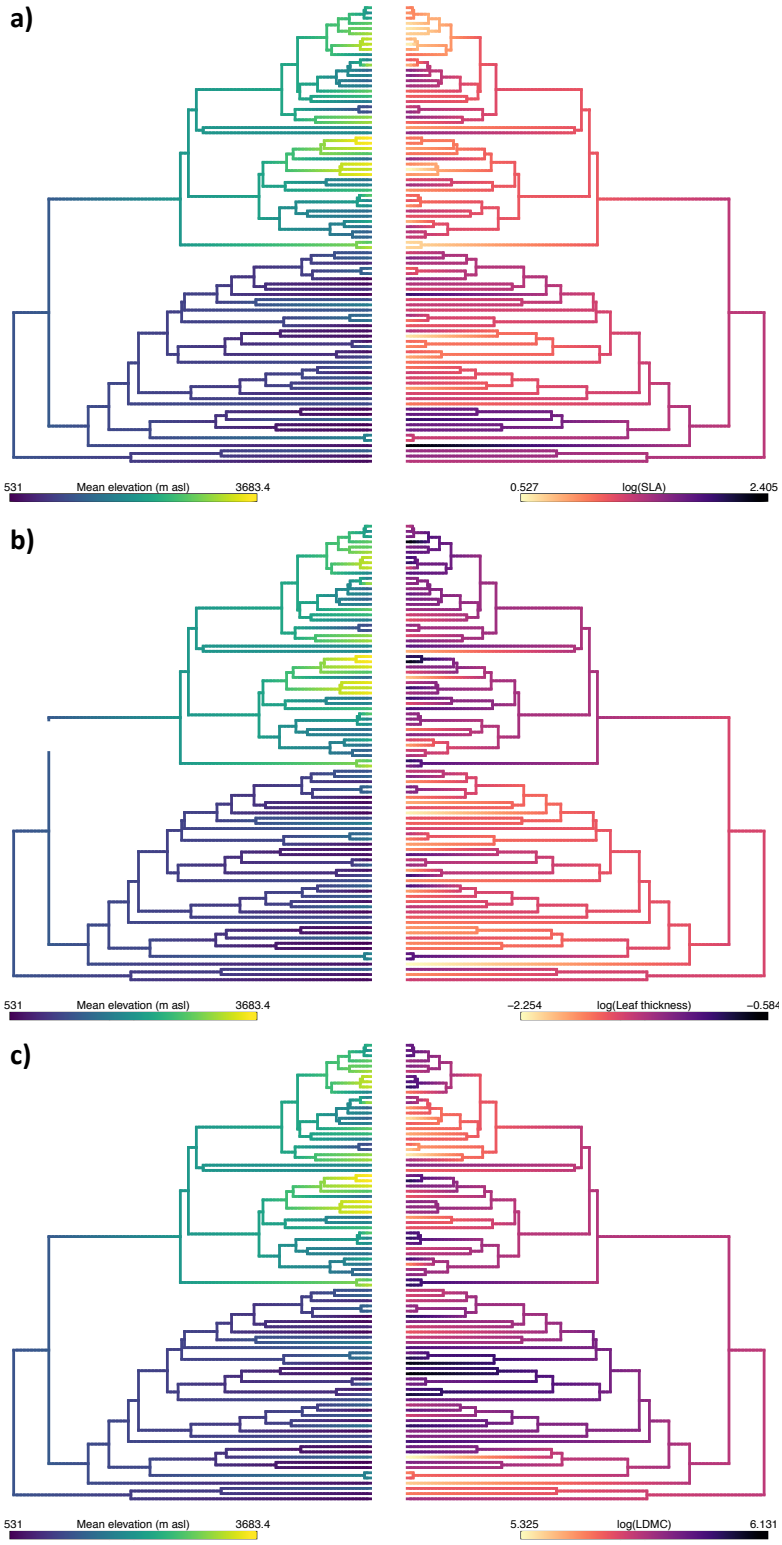

Figure 4.4: Paired phylogenies of 88 species within the tribe Miconieae allowing comparison of species mean elevational distribution and functional leaf trait values by which branch lengths are coloured. Left side phylogenies in a-c represent species' mean elevations. Right side phylogenies represent **a)** specific leaf area (logSLA), **b)** leaf thickness (log), **c)** leaf dry matter content (logLDMC). Species mean elevation, SLA, leaf thickness, and LDMC all display phylogenetic signal.

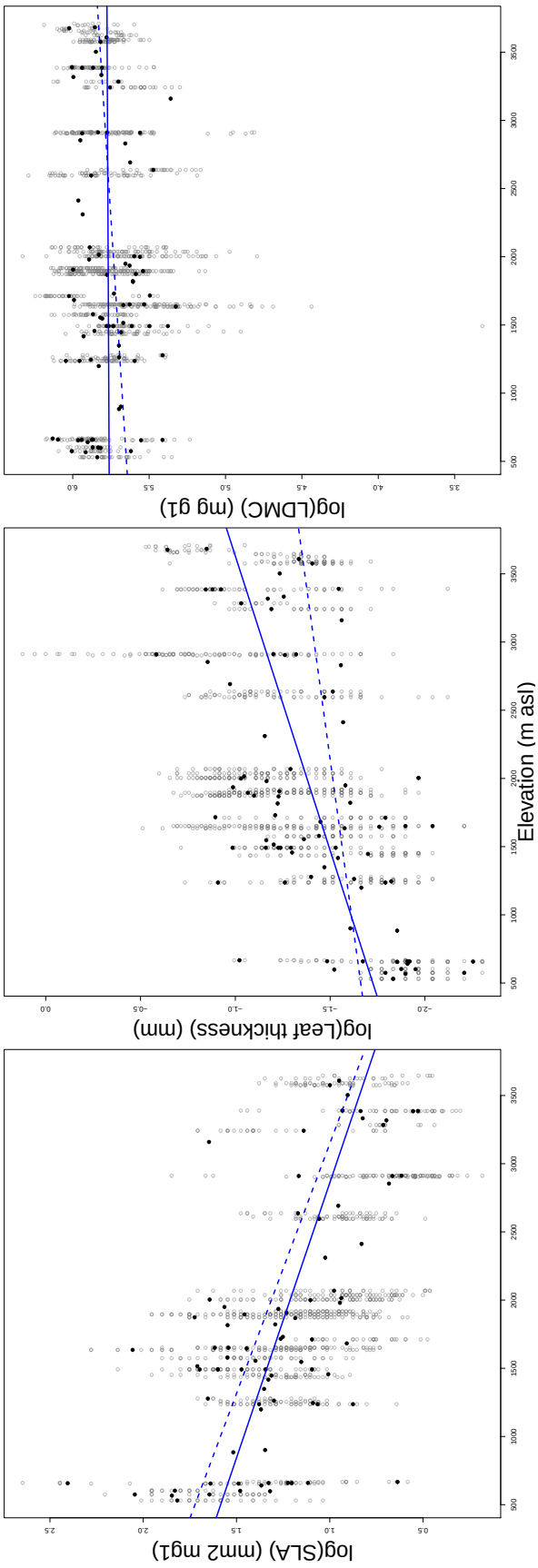

Figure 4.5: Elevational trends among Miconieae species functional leaf traits and the influence of phylogenetic relationships. Grey points indicate individual leaf values, black points indicate species mean values. Based on mean values solid blue lines indicate linear regressions, dashed lines indicate phylogenetic generalised least squares (PGLS). **a)** significant correlation between species mean log SLA and species mean elevation (R^2 = 0.36, p <0.001) holds when accounting for phylogeny (R^2 = 0.28, p <0.001), **b)** significant correlation between species mean log leaf thickness and species mean elevation (R^2 = 0.35, p <0.001) does not hold when accounting for phylogeny (R^2 = 0.02, p = 0.1), and **c)** no correlation between species mean log LDMC and species mean elevation (R^2 = −0.01, p = 0.46) becomes a weakly significant correlation once phylogeny is accounted for (R^2 = 0.05, p <0.05).

elevation (R^2 = 0.36, p $<$0.001; Figure 4.5a). Species mean log leaf thickness shows a positive correlation with species mean elevation (R^2 = 0.35, p $<$0.001; Figure 4.5b). Species mean log LDMC shows no correlation with species mean elevation (R^2 =$-$0.01, p = 0.46; Figure 4.5c). Applying PGLS analyses to those traits displaying phylogenetic signal, we find correlations between functional leaf traits and elevation vary in the potential influence of interspecific autocorrelation due to phylogenetic relationships (Table 4.3). We find the significant correlation between species mean log SLA and species mean elevation (R^2 = 0.36, p $<$0.001) holds when accounting for phylogeny (R^2 = 0.28, p $<$0.001) (Figure 4.5a). In contrast we find that the significant correlation between species mean log leaf thickness and species mean elevation (R^2 = 0.35, p $<$0.001) does not hold when accounting for phylogeny (R^2 = 0.02, p = 0.1) (Figure 4.5b). We find that the non-significant correlation between log LDMC and elevation (R^2 = $-$0.01, p = 0.46) becomes weakly significant once phylogeny is accounted for (R^2 = 0.05, p $<$0.05, Figure 4.5c).

4.5 Discussion

Our results suggest that, treating Miconieae as a test lineage, elevational diversity trends and phylogenetic constraints on elevational distribution at the species-level largely match those observed at the genus-level in the broader community (Chapters 2 and 3). Within TMF, the taxonomic and evolutionary diversity of Miconieae at mid-elevations is as high, or higher, than diversity in the lowlands, with closely related species tending to occur at similar elevations. We additionally find patterns within Miconieae, of decreasing specific leaf area (SLA) and increasing leaf thickness, which are consistent with global trait patterns. SLA, leaf thickness, and leaf dry matter content (LDMC) display phylogenetic signal. Further, we find evidence that the elevational position of species and their leaf functional traits may share an evolutionary association. However, further work is needed to determine whether traits act to determine and constrain the elevations at which species are able to occur.

The shape of the elevational diversity trend, observed here within Miconieae, supports a peak in taxonomic and phylogenetic richness at mid-elevations, therefore sharing some consistency with broader genus-level patterns (Chapter 3). In contrast with genus-level patterns, support for a mid-elevation peak is strongest in taxonomic richness, while the weaker evidence of a mid-elevation peak in evolutionary diversity is more comparable to the trend within angiosperms alone (Chapter 3 - supplementary material), rather than to the stronger trend observed when including all tree taxa (i.e., angiosperms, gymnosperms and tree ferns). Within the Miconieae lineage, we also find that PD and TILD measures of evolutionary diversity give more similar results that at the genus-level. Given the different weighting of evolutionary depth between PD and TILD, this similarity of pattern in Miconieae may be due to the absence of deeply diverging, yet species-poor lineages, such as the gymnosperm and tree fern lineages, which are present in the full genus level analysis. In other words, the Miconieae phylogeny is more balanced than the genus-level phylogeny encompassing the whole tree flora along the transect.

Considering the Melastomataceae family more generally, our results are consistent with a humped-shape elevational richness trend observed in the Bolivian Andes (Kessler, 2000), yet deviate from a monotonic decrease in richness observed along a Costa Rican elevation gradient (Kandlikar et al., 2018). The decrease in richness observed in Costa Rica, may be due to an absence of sampling between 800 and 2000 m asl, which are the elevations at which we find some of the highest richness values for our metrics. Alternatively, the Miconieae clade that tends to have distributions at mid to high elevations along our gradient could represent an Andean divergence which is absent, or less diverse in Central America. It must also be noted that our observations of Miconieae richness show substantial variability among plots at similar elevations, suggesting that elevation itself explains less variation in richness at the species level within this lineage than at the broader genus-level. This species level variation may in part be explained by the highly heterogeneous nature of the montane forest landscape and/or differences in the plot sizes. The 1-ha plots quantifying genus level rich-

ness may be less likely to be influenced by small scale topographic heterogeneity or edaphic variation than the 0.01-ha plots used here for Miconieae. Topographic factors are known to substantially influence general richness patterns (Körner, 2000; Stein et al., 2014), while edaphic gradients have been shown to influence species turnover within Melastomataceae (Ruokolainen et al., 1997).

Despite the exceptionally broad elevational range occupied by the lineage, Miconieae species along this TMF elevation gradient tend to display the same trend for complete taxonomic turnover and narrow elevational ranges (Figure 4.3) that is evident among genera (Chapter 2). Further matching genus-level trends, we find significant phylogenetic signal for mean elevation, meaning closely related species tend to occur at similar elevations. In contrast we find no phylogenetic signal for elevational range size. While most species are restricted to very narrow elevational ranges (47% of species were only found at a single elevation), the few broadly distributed species occur randomly across the phylogeny. The reflection of genus-level trends, even within a lineage such as Miconieae, which occupies an unusually broad elevational range, shows that in terms of a generalisable pattern of evolutionary constraint on elevational distributions, the exceptions may prove the rule.

While the observed pattern of co-occurrence in closely related Miconieae species might be expected under phylogenetic niche conservatism, it clearly does not support the expectations of competitive exclusion, i.e. that close ecological similarity at the species level precludes coexistence (Macarthur and Levins, 1967; Cavender-Bares et al., 2009). However, it has been suggested that within vegetation types which have undergone recent diversification, co-occurring species are more closely related than expected (Procheş et al., 2006). In evolutionary terms, the Andean uplift is a recent event, and the tropical montane forests of the Andes are considered as a centre of diversification (Hughes and Eastwood, 2006). Moreover, many species within Miconieae may be recently diverged, with several genera within the tribe displaying exceptionally elevated speciation rates (Berger et al., 2016).

In addition to consistency between species and genus-level elevational diversity and distribution patterns, we find that changes in functional leaf traits with elevation within Miconieae are comparable to broader trait-environment associations (Read et al., 2014; Reich, 2014). We observe a decrease in mean species SLA with elevation which matches previous observations within Melastomataceae (Kandlikar et al., 2018), the general trend along our gradient (van de Weg et al., 2009), as well as the broader global pattern (Read et al., 2014). However, the elevational decrease in SLA observed here, and more broadly within Melastomataceae, appears to be weaker than the global angiosperm trend (Read et al., 2014). A further pattern within our results for Miconieae, suggests greater variability in species mean SLA values below c.2000 m asl. Lower trait variation at higher elevations agrees with expectations of stronger environmental filtering in harsher environments (Chase, 2007; Marx et al., 2017), where a narrower range of trait strategies may be successful. We observe an elevational trend for leaf thickness which is the inverse of SLA. Within Miconieae, leaf thickness increases with increasing elevation. Given leaf thickness is frequently correlated with SLA (Poorter et al., 2009), it is perhaps unsurprising that given an elevational pattern in one trait, a pattern exists in the other. Either way, placed in the context of the global leaf economic spectrum (Wright et al., 2004; Díaz et al., 2016), the elevational trait trends of Miconieae match the general trend towards fast, resource-acquisitive species at lower elevations versus slow, resource-conservative species at higher elevations (Read et al., 2014).

Further to the observed trait patterns across elevation, we find significant phylogenetic signal for both SLA, leaf thickness, and LDMC suggesting that closely related species within Miconieae have similar resource investment strategies. Evidence of phylogenetic signal for both elevational distribution and functional traits matches the expectations of phylogenetic niche conservatism, though it does not definitively establish a causal relationship between traits and distribution as expected by environmental filtering. For example, applying a phylogenetic generalised least squares (PGLS) analysis, we find the correlative relationship between species' elevational distribution and

species' leaf thickness is not any greater than would be expected under a Brownian motion (BM) model of evolution. As such, the correlation may be coincidental and an artefact of phylogenetic relationships and phylogenetic signal for one or both characteristics. In contrast, the correlative trend between SLA and elevational distribution holds even when phylogenetic relationships are accounted for. Therefore, species elevational distributions and SLA may be associated, undergoing correlated evolution.

Despite the above patterns, elevational trait patterns are not uniform within Miconieae. For leaf dry matter content (LDMC), we do not find an elevational pattern across elevation, though significant phylogenetic signal is found. LDMC has been suggested as a more reliable predictor of resource investment strategies than SLA, as it is less variable across replicates and, unlike SLA, is largely independent of leaf thickness (Wilson et al., 1999). The absence of an elevational pattern, yet presence of phylogenetic signal in LDMC, therefore suggests drawing conclusions about functional strategies and trait-distribution associations from SLA and leaf thickness trends must be done with caution. While there is strong support in the literature for an association between functional traits and species' distribution (Hulshof et al., 2013; Read et al., 2014; Bruelheide et al., 2018) traits that are measured are often just the 'easiest' ones, with more relevant or more 'functional' ones potentially unmeasurable or overlooked (Baraloto et al., 2010; Hortal et al., 2015). Moreover, variation between species may be driven by multiple traits (Cornelissen et al., 2003). Indeed, closer inspection of the occurrence of SLA across our Miconieae phylogeny (Figure 4.4a) shows that low SLA, low elevation species are not the closest relatives of low SLA, high elevation species, which might be expected if species first had to evolve low SLA prior to colonizing higher elevations. This suggests that the low SLA values in high elevation species were acquired at the same time, or after, species populated high elevations. SLA may simply track elevational shifts, rather than facilitate them. It may be that other, unmeasured traits are involved in determining species elevational distributions.

Overall, our observations within Miconieae, along with similar trends observed at the genus-level across a breadth of plant lineages (Chapter 2), suggests that phylo-

genetic signal for elevational distribution may be a ubiquitous trend among the woody plant taxa of tropical montane forests. In addition, within Miconieae, high taxonomic and evolutionary richness at mid-elevations matches the genus-level pattern and reinforces the biodiversity significance of mid-elevation montane forests. Middle elevations may form an important mingling point for montane and lowland lineages with distinct evolutionary histories. Finally, we demonstrate that functional leaf traits vary predictably with elevation and are associated with species elevational distributions. Leaf traits which reflect the leaf economic spectrum undergo correlated evolution with species elevational distributions, yet different traits, unmeasured or unrelated to resource-investment strategy, may be more significant mechanistic drivers of the constrained distributions of taxa across this tropical montane elevation gradient.

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4.A Appendix

Table 4.2: Phylogenetic signal for elevational distributions and function leaf traits within Miconieae comparing between Pagel's Lambda and Blomberg's K.

	Phylogenetic signal			
	Lambda	**p-value**	**K**	**p-value**
Mean elevation	0.84	<0.001	0.65	0.001
Elevational range	0.00007	1	0.15	0.371
logSLA (mm^2 mg^1)	0.8	<0.001	0.44	0.001
logLDMC (mg g^1)	0.88	<0.001	0.39	0.001
logLeaf thickness (mm)	0.4	<0.001	0.31	0.001

Table 4.3: Elevational trends in functional leaf traits a comparison between linear regression and phylogenetic least squares (PGLS). Slope estimate represents change in leaf trait value per 1 metre elevation (+/- standard error). p-values: *** <0.001, ** <0.01, * <0.05.

	PGLS		Linear regression	
	R^2	**Slope estimate**	**R^2**	**Slope estimate**
logSLA (mm^2 mg^1)	0.28	-0.0003 (±0.00005)***	0.36	-0.0003 (±0.00004)***
logLDMC (mg g^1)	0.05	0.00006 (±0.00003)*	-0.01	0.000004 (±0.00002)
logLeaf thickness (mm)	0.02	0.0001 (±0.00006)	0.35	0.0002 (±0.00003)***

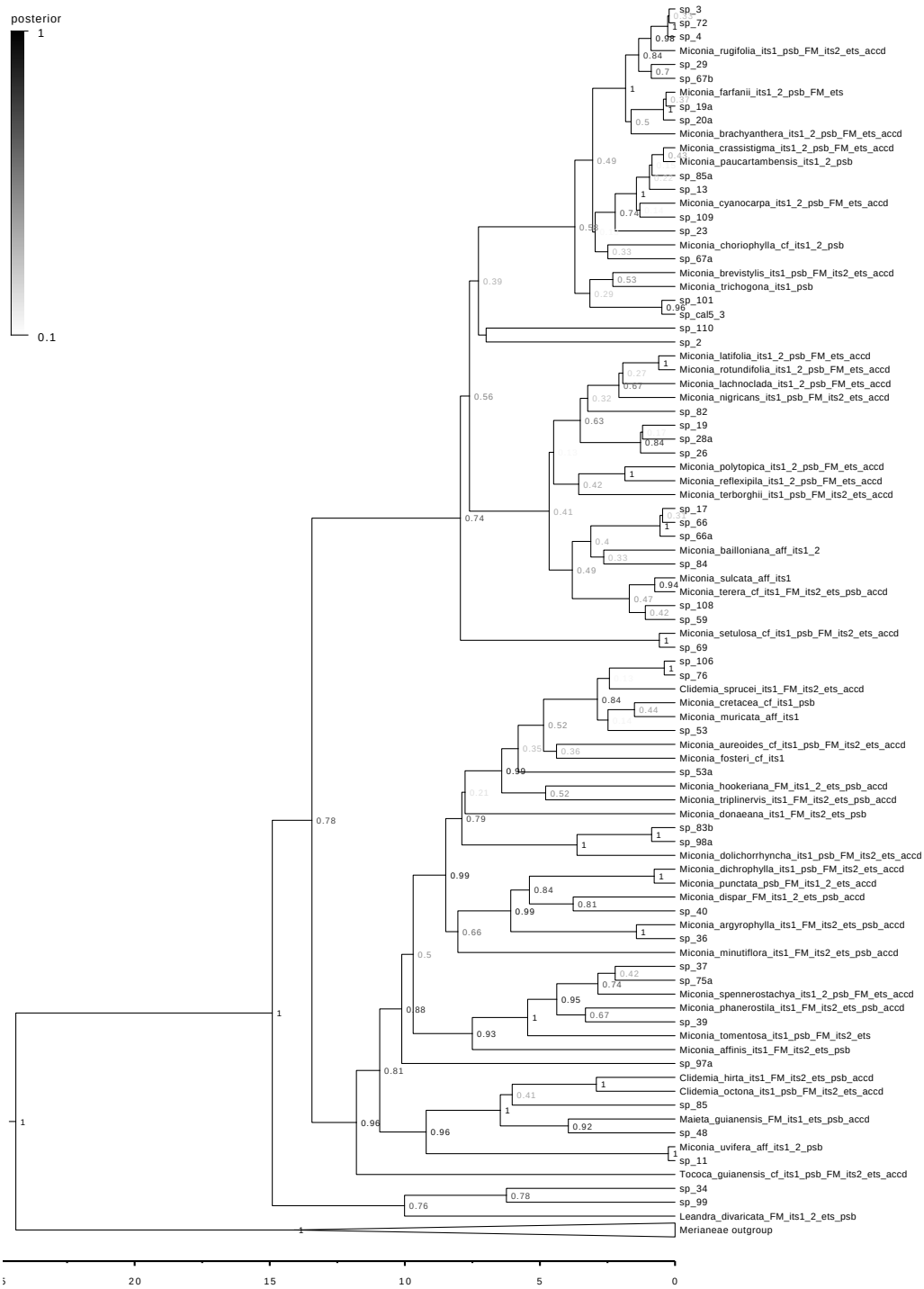

Figure 4.6: A time calibrated, maximum clade credibility phylogeny for 88 species within the plant tribe Miconieae, plus a Merianeae outgroup. Values in nodes indicate posterior support values shaded by strength of support as indicated by the legend, light = weak support, dark = strong support. X-axis indicates evolutionary age in millions of years.

Chapter 5

Synthesis and conclusions

The principle motivation of this thesis was to contribute towards a deeper understanding of the role evolutionary constraint plays in shaping the elevational distributions and diversity patterns of woody plants within tropical montane forests. I firstly combined plot inventory data from an Amazon-to-Andes elevation gradient, spanning from 425 to 3625 m asl, with a genus-level phylogeny representing a breadth of vascular plants from angiosperms and gymnosperms, to pteridophyte tree ferns. To assess the generality of genus-level trends across evolutionary scales, I then conducted independent and detailed sampling of species within the plant tribe Miconieae. I additionally made leaf traits measurements that represent the leaf economics spectrum (Wright et al., 2004), facilitating a deeper examination of the factors driving elevational distribution patterns. Ultimately, the aim of this research was to determine whether evolutionary processes are associated with the narrow elevation distributions common among tropical montane forest taxa. In this concluding chapter I review the key findings of the empirical studies presented in Chapters 2 to 4, and synthesise results in the context of the four core science questions set out in the introduction to this thesis:

1. **Does evolutionary history influence the elevational distribution of woody plant taxa?**

2. **Does evolutionary history shape patterns of evolutionary diversity and richness over elevation?**

3. **Are elevational distribution and diversity trends consistent across evolutionary scales?**

4. **Do functional trait trends have an evolutionary association with species' elevational distributions?**

I then evaluate the wider implications of this research, discuss potential future developments to the work, and finally provide some concluding remarks.

5.1 Key findings

Question 1: Does evolutionary history influence the elevational distribution of woody plant taxa?

- Closely related evolutionary lineages tend to occupy similar elevational distributions, with most taxa only occurring over narrow ranges.
- The mid-elevation cloud-base ecotone may form an environmental threshold separating evolutionarily distinct montane and lowland floras.
- Broad elevational distribution, though uncommon, is not evolutionarily constrained within lineages, arising across the plant phylogeny.

Evolutionary hypotheses based on phylogenetic niche conservatism (Wiens and Graham, 2005; Losos, 2008; Wiens et al., 2010) expect closely related taxa to be ecologically similar and occur in similar environments (Wiens and Donoghue, 2004). Yet potential evolutionary patterns underlying the distribution of tropical montane forest biodiversity are unclear. Chapter 2 of this thesis demonstrated that, across angiosperm, gymnosperm, and tree fern lineages, evolutionary history influences elevational distributions. Closely related genera tend to occupy similar elevational distributions within tropical montane forest.

Additionally, with phylogenetic clustering of closely related genera both above and below the cloud-base ecotone, this transition zone may represent an environmental threshold, limiting taxa distributions and separating montane and lowland floras with distinct evolutionary histories. Greater phylogenetic clustering above the cloud-base ecotone suggests that tropical montane cloud forest may be a tough environment, where environmental filtering exerts a stronger influence on which taxa are able to persist.

An exceptional few genera occupy broad elevational distributions. The lack of phylogenetic signal for occurrence across a large gradient of environmental variation gra-

dient suggests that the ability to evolve broad environmental tolerance is not clearly restricted to certain lineages. Nonetheless, most genera occupy narrow elevational ranges, and the timescale necessary for adaptation to different environmental conditions is likely to be incompatible with ongoing rapid change (Bush et al., 2004; Feeley et al., 2011; Pepin and Mountain Research Initiative EDW Working Group, 2015).

In Chapter 4, an evolutionary influence on the distribution of species within the plant tribe Miconieae was revealed, with closely related species tending to be found at similar elevations. Phylogenetic signal for elevational position in Miconieae is high, such that the majority of species occupying high elevations are from a single evolutionary clade. Most species occupy narrow elevational ranges with nearly 50% of species only recorded at a single elevation.

Question 2: Does evolutionary history shape patterns of evolutionary diversity and richness across elevation?

- The elevational diversity gradient within tropical montane forest is not a simple linear decrease, but rather a non-linear trend with variation between taxonomic and phylogenetic richness measures.
- The unique floral diversity of the mid-elevation tropical montane forests may rival that found in the tropical lowlands, especially when quantifying diversity in terms of the total evolutionary history represented by taxa at a given elevation.
- High evolutionary diversity at mid-elevations may be the result of a meeting and mingling of the evolutionarily distinct tropical montane and tropical lowland floras.

The environmental variation occurring along elevation gradients provides an opportunity to examine the drivers of spatial variation in diversity. Attempts to explain large-scale diversity patterns, such as the latitudinal and elevational diversity gradients, have resulted in many competing and divergent theories (Currie et al., 2004; Wiens and Donoghue, 2004; Mittelbach et al., 2007; Segovia and Armesto, 2015).

From an evolutionary perspective, the Tropical Niche Conservatism and Out of the Tropics Hypotheses have been prominent, and predict decreasing richness, evolutionary diversity and evolutionary age with increasing elevation (Wiens and Donoghue, 2004; Jablonski et al., 2006).

Chapter 3 of this thesis, focusing on tropical montane tree genera, revealed taxonomic and phylogenetic patterns of diversity across elevation that are non-linear, with a general trend for diversity at mid-elevations that is equivalent or greater than that found at lower elevation. Diversity then decreases towards higher elevation. Chapter 4 showed that for species within the plant tribe Miconieae, variation in diversity within tropical montane forests may be less strongly shaped by elevation. However, a pattern showing high levels of both taxonomic and phylogenetic diversity at mid-elevations is still supported.

Findings within Chapter 3 also show that evolutionarily older lineages tend to be more numerous at middle to high elevations, while many evolutionarily younger lineages are restricted to lower elevation distributions. The results match previous observations based on mean family ages (Segovia and Armesto, 2015; Tiede et al., 2015). However, the analysis presented in this thesis, based on phylogenetic depths may provide a more meaningful quantification of how the evolutionary structure of communities' actually changes across elevation.

The mid-elevation tropical montane forest can be thought of as an evolutionary mixing pot. Our results suggest that the distinct evolutionary histories of the unique tropical montane and tropical lowland flora (Segovia and Armesto 2015; see also Chapter 2 and Chapter 4), may meet and mingle at mid-elevations, driving a peak in diversity that is especially evident when the full evolutionary depth of the tropical montane tree community is considered. Overall, the findings presented in this thesis do not support the expectations of either the Tropical Niche Conservatism or Out of the Tropics hypotheses, that the TMF flora constitutes a recently derived and depauperate subset of lowland tropical diversity. The findings presented in this thesis show that the

evolutionary diversity of mid-elevation tropical montane forests trees can rival that of the tropical lowlands.

Question 3. Are elevational distribution and diversity trends consistent across evolutionary scales?

- The trend for evolutionarily close relatives to occupy similar elevational distributions may be a ubiquitous trend across the woody plant taxa of tropical montane forests.
- A trend for high taxonomic and evolutionary diversity at mid-elevations is supported at genus and species scales.
- At deeper evolutionary scales a greater number of lineages are found at middle to high elevations. At shallower evolutionary scales the greatest number of lineages occur at a lower elevation.

Many ecological patterns are contingent on the scale of study, and the search for general rules is a common ambition (McGill, 2019; Rapacciuolo and Blois, 2019). Species level identifications are often difficult in tropical plants (Dexter et al., 2010). As such many analyses are conducted at higher taxonomic ranks (Gaston and Williams 1993; Coelho de Souza et al. 2016; Dexter and Chave 2016; Chapters 2 and 3. However, genus-level analyses are potentially misleading, particularly in evolutionary studies (Smith and O'Meara, 2009). Therefore Chapter 4 of this thesis presented detailed consideration of species-level trends within the tribe Miconieae, which can be compared against the genus-level analyses of Chapter 2 and Chapter 3. The trend for closely related taxa to occupy similar elevations was observed at both genus (see Chapter 2) and species scales (see Chapter 4). Moreover, though at the genus-level, *Miconia* (the largest genus within Miconieae) is one of a few exceptional genera occupying a broad elevational range, the species level trend within this genus matches the genus-level trend. Exceptions may prove the rule, and evolutionary conservatism of elevational distribution may be a ubiquitous trend across the woody plant taxa of

tropical montane forests.

The genus-level trend for high levels of diversity at middle elevations (see Chapter 3), is broadly supported by the species-level trends in Miconieae (see Chapter 4). In the species-level analysis, elevation explains less variation in diversity, which may reflect random sampling effects resulting from smaller scale plots. At species-level lower variation in the shape of the elevational diversity gradient among metrics than at the genus-level, may be the result of a more temporally balanced phylogeny, uninfluenced by a few lineages deeper in evolutionary time.

Further, a section of analysis presented in Chapter 3 moves away from utilising taxonomic ranks to study evolutionary diversity patterns. Elevational diversity across evolutionary scales was considered in terms of patterns at different evolutionary time slices, with evidence that lineages at deeper evolutionary time slices are more numerous at middle to high elevations, while many lineages at shallow evolutionary time slices are restricted to lower elevations.

Question 4. Are species' elevational distributions associated with evolutionary patterns in functional traits?

- Specific leaf area and leaf thickness vary predictably with elevation within tropical montane forests, matching the expectations of global trait-environment trends.
- Closely related species tend to have similar functional leaf trait values.
- Functional leaf traits, associated with the global leaf economic spectrum (LES), share an evolutionary association with species' elevational distributions. Yet unmeasured traits, or those unrelated to the LES may be of greater importance in determining species' elevation distributions.

Functional leaf traits can be placed in the context of a spectrum of fast to slow ecological strategies (Wright et al., 2004), and the link between traits and environment is well known (Reich, 2014; Bruelheide et al., 2018). Thus, trait patterns and their evo-

lutionary associations may provide a mechanistic explanation for species elevational distributions. Closely related species may occur at similar elevations because they possess similar traits. Within Chapter 4 of this thesis the elevational and evolutionary patterns of functional leaf traits were investigated for the tribe Miconieae. It was revealed that within this lineage, specific leaf area (SLA) decreases with elevation and leaf thickness increases with elevation, matching the trends of global trait-environment relationships (Read et al., 2014; Reich, 2014). In addition, SLA, leaf thickness and leaf dry matter content (LDMC) show phylogenetic signal, meaning closely related species tend to have similar leaf trait configurations. Taking into account potential interspecific autocorrelation due to phylogenetic signal for leaf traits and species elevational position, only the elevational trend in SLA holds strongly. When species occur at high elevation it seems they also tend to have low SLA values. While these findings within Miconieae, suggest species' SLA and elevational distributions may undergo correlated evolution, identifying a causative link between functional traits and elevational distribution requires further research. It may be that traits other than those associated with the global leaf economic spectrum (Wright et al., 2004), are the most mechanistically important determinants of species' elevational distributions in tropical montane forests.

5.2 Wider implications

Elevation gradients are considered to provide natural laboratories for understanding the impact of changing environmental conditions (Malhi et al., 2010). As such elevation provides a means for examining variation in the drivers and trends of biodiversity distribution in different environments. The work presented in this thesis adds to the body of work showing that evolutionary factors, such as phylogenetic niche conservatism (Wiens and Donoghue, 2004; Wiens and Graham, 2005), provide an important lens through which to understand the spatial organisation of biodiversity. Further, an evolutionary perspective of the distribution of taxa across different environments may prove relevant to our understanding of ecological responses to global change.

Ongoing environmental change is impacting species distribution patterns across the planet (Pauli et al., 1996; Walther et al., 2005; Parmesan, 2006). With warming of 1.8 – 5.1^{o}C predicted to occur across the tropical Andes during the next century (Urrutia and Vuille, 2009), there is a high likelihood of detrimental consequences for the biodiversity of neotropical montane forests (Bush et al., 2004; Feeley and Silman, 2010a,b). Tropical montane forests comprise about 8% of the tropical forests globally, yet those in the Andes alone contain at least 20,000 endemic species of vascular plants – or 6.7% of global plant diversity (Myers et al., 2000). These forests hold additional broader importance, providing water to large parts of the world's population (Mittermeier et al., 2005; Bruijnzeel et al., 2011).

With evolutionary constraint of biodiversity distribution to generally narrow elevational ranges seemingly ubiquitous across woody plant lineages within tropical montane forest, any substantial changes to environmental conditions at particular elevations may result is a disproportionate loss of evolutionary diversity and history. For example, if there are major changes to the cloud dynamics (Still et al., 1999; Helmer et al., 2019) that are a fundamental feature of tropical montane cloud forests (Foster, 2001) many of the unique species and evolutionary lineages restricted to this environment could disappear. Further, with clear evolutionary trends in functional trait patterns across the ecological variations of elevation, substantial environmental change may shift the functional composition of communities. For example, a reduction in cloud immersion and rainfall, and an increase in temperature, may push the functional nature of the plant community within tropical montane cloud forest towards faster-growing, resource-acquisitive species (Helmer et al., 2019). Such diversity and functional changes hold concern not only in terms of conservation, but also in terms of the ecosystem services provided by the unique and vulnerable forests.

5.3 Future research directions

The research presented across this thesis demonstrates that evolutionary trends and tendencies are associated with woody plant diversity and distribution patterns across the elevational variation of tropical montane forests. However, the findings reported in the empirical studies in Chapters 2 to 4 raise further questions, with a number of possible extensions and expansions to this work. A few potential future directions for research are summarised below:

5.3.1 Elevational extensions and geographic dimensions

The elevation gradient that provides the focus of this thesis is extensive and reaches 3625 m asl. Yet elevation does not stop at the top of the montane forests. For example, in the Neotropics high-elevation montane grasslands reach $>$4500 m asl (Veblen et al., 2015). While the influence of the cloud-base ecotone as a significant environmental threshold was discussed at various stages within this thesis, research into evolutionary patterns in lineage distributions across the even starker threshold of the treeline would be of interest. Above the treeline, away from the insulating qualities of the forest canopy, freezing temperatures are frequent. Freeze tolerance is thought to be a major driver of species distribution trends globally, especially within plants (Zanne et al. 2014; Segovia et al, in review), and is likely to be reflected in evolutionary distribution trends at elevations above the treeline. In this context, the lineage specific focus on Miconieae in this thesis might be extended to several shrubby and prostrate species of the lineage occurring in high-elevation grasslands.

A further extension to the elevational focus of this thesis is a comparison of elevational and geographic range patterns. A broadly exercised comparison is that made between elevational and latitudinal patterns (Stevens, 1992; Swenson and Enquist, 2007; Qian and Ricklefs, 2016). While trends across elevation and latitude may be distinct, especially in the tropics (Rahbek, 1995), comparisons across geographic dimensions may reveal ecological insights. For example, as discussed in Chapter 2 and

Chapter 4, the plant family Melastomataceae includes genera such as *Miconia*, which displays an exceptionally broad elevational range. Yet in terms of geographic range, genera within the family have lower mean range size than expected by chance (Dexter and Chave, 2016). The drivers of this contrast between elevational and geographic range size within the Melastomataceae are unclear and it is possible that *Miconia* is simply an exception to general trends. Yet broader comparison of elevational vs geographic range sizes across lineages might reveal similar contrasts in other lineages and compel deeper mechanistic analysis.

5.3.2 Intraspecific trends and further traits

While this thesis considered elevational trends in functional leaf traits at the species-level (Chapter 4), further trait-based study could be conducted at the intraspecific level. Though uncommon, a few species occur over substantial elevational ranges, yet it is unclear why they are able to do so. There could be a relationship between trait plasticity and breadth of elevational distribution. An associated research question might be 'Do functional trait values show greater variation within broadly distributed species than in narrowly distributed species?' A limited number of functional traits were quantified within this thesis, and they may not represent the most important functional drivers of elevational distribution (Baraloto et al., 2012; Hortal et al., 2015). Moisture availability has been demonstrated as the major driver of montane forest change on a paleoecological time scale (Urrego et al., 2010). As such, analyses based on traits, such as foliar water uptake (Eller et al., 2016) and leaf wettability (Goldsmith et al., 2017), associated with adaptation to the different moisture regimes encountered within tropical montane forest may provide greater functional insights. Further, trait measurements encompassing some of the other axes of plant form and function, such as the wood economic spectrum (Chave et al., 2009), would also provide a more complete analysis of the functional trends across tropical montane forests.

In terms of the lineage specific focus of Chapter 4, the trends observed here could be fit into the broader phylogenetic context of Miconieae (Michelangeli et al., 2004)

while additional large-scale analysis of evolutionary trends in trait-environment associations within the lineage could be achieved by combining distribution data from the Global Biodiversity Information Facility (GBIF; www.gbif.org) and trait data from the TRY plant trait database (www.try-db.org), with the existing, and developing understanding of Miconieae phylogenetic relationships (Michelangeli et al., 2004).

5.3.3 Biogeographic scales and gradient replication

Ultimately, one of the clearest caveats to the findings of this thesis is that they represent only the patterns along a single elevation gradient. Montane landscapes are highly heterogenous and frequently comprise unique, endemic biota, which could result in idiosyncratic patterns and trends. There is a need to establish whether single gradient trends hold at broader biogeographic scales. As such, future research efforts should be directed towards making replicable observations along comparable gradients. A pertinent example is the cloud-base ecotone. The elevations at which frequent cloud immersion occurs shows great regional and even local variation (Foster, 2001). Across the elevation gradient studied in this thesis, the cloud-base generally forms between 1500 and 2000 m asl. However, cloud immersion is unlikely to be the only factor influencing the discernible ecological and evolutionary patterns occurring around these elevations. For example, mid-elevations may simply represent a broader elevational limit for lowland amazon taxa adapted to a cooler climate during the Quaternary (Silman, 2007), rather than an effect of the cloud-base per se. In order to confidently ascribe observations, such as phylogenetic clustering above and below the cloud-base, patterns must be analysed across multiple gradients with variation in the elevation of the cloud-base ecotone.

Established continental-scale collaborations exist for other important ecosystems, such as Tropical Rainforests (e.g. RAINFOR - www.rainfor.org) and Seasonally Dry Tropical Forests (e.g. DryFlor - www.dryflor.info). Tropical montane forests remain difficult and complex environments to access and conduct research in and a large-scale integrated network of gradients and researchers has been slower to form. How-

ever, the recent establishment of the international working group, sANDES, based at the German Centre for Integrative Biodiversity Research iDIV (www.idiv.de), along with precursors Martin and Bellingham (2016); Fadrique et al. (2018), suggests that a deeper, biogeographic scale understanding of the unique ecological and evolutionary nature of tropical montane forests may be on the horizon.

5.3.4 Species unknown to science

The biodiversity of tropical montane forests is recognised as being globally exceptional (Myers et al., 2000; Mutke and Barthlott, 2005), yet they remain understudied and under explored. Continuing and more widespread collecting effort is necessary to reliably quantify the diversity and distributions of species within these unique environments (Feeley and Silman, 2011). Given the complexity of terrain, limited geographic extent of previous research, and high levels of diversity and endemism in tropical montane forests, there are likely many more species unknown to science awaiting discovery. Indeed, even within relatively well researched areas new discoveries are frequently made. Collections made during the fieldwork component of this thesis contributed material to the recent description of a new species, *Miconia paucartambensis* (Burke and Michelangeli, 2018), and form the basis for a further new species description currently in preparation (Griffiths et al, in prep).

5.4 Concluding remarks

The research presented in this thesis adds to the growing body of work showing that evolutionary processes are important shapers of the spatial organisation of biodiversity. Within tropical montane forests, factoring in the complete evolutionary depth of the tree community shows that middle-elevations house greater evolutionary diversity than lower elevations. This diversity peak is likely driven by the mixing and mingling of unique montane forest flora and lowland floras with distinct evolutionary histories and varying evolutionary age structures. Elevational distribution shaped by evolutionary

history, may be near ubiquitous within the woody plant lineages of tropical montane forests. However, a truly mechanistic understanding of the limits on elevational distribution remains unclear.

Under ongoing environmental change, where necessary rates of migration may be unachievable for sedentary plants, the ability to adapt or acclimate will be essential for survival. However, in tropical montane forest, with evolutionary heritage shaping ecological strategies and elevational distributions, the fundamental temporal mismatch between evolutionary processes and environmental change may heighten the vulnerability of this ecosystem. If the value of montane forests along the Amazonian flank to the Andes is not truly appreciated, the evolutionary processes which may have shaped their unique and exceptional biodiversity, may now leave it a greater risk of being lost.

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Pl. 40.
MELASTOMA punctata.
Poiteau pinx.t
De l'Imprimerie de Langlois
Langlet sculp.